

Advancing biological invasion hypothesis testing using functional diversity indices

D Renault, Manon C.M. Hess, Julie Braschi, Ross N Cuthbert, Marta Gaia Sperandii, Manuele Bazzichetto, Olivier Chabrerie, Gabrielle Thiébaut, Elise Buisson, Frédéric Grandjean, et al.

▶ **To cite this version:**

D Renault, Manon C.M. Hess, Julie Braschi, Ross N Cuthbert, Marta Gaia Sperandii, et al.. Advancing biological invasion hypothesis testing using functional diversity indices. Science of the Total Environment, 2022, 834, pp.155102. 10.1016/j.scitotenv.2022.155102 . hal-03638923

HAL Id: hal-03638923
https://amu.hal.science/hal-03638923

Submitted on 1 Jun 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Science of the Total Environment 834 (2022) 155102

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Review

Advancing biological invasion hypothesis testing using functional diversity indices

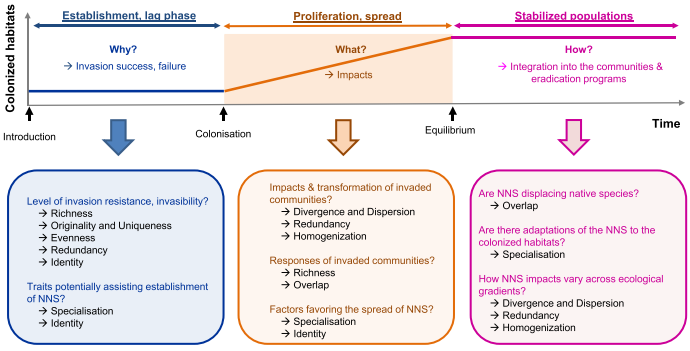
David Renault [a,b,*], Manon C.M. Hess [c,d,e], Julie Braschi [c,f], Ross N. Cuthbert [g,h], Marta G. Sperandii [i], Manuele Bazzichetto [a], Olivier Chabrerie [j], Gabrielle Thiébaut [a], Elise Buisson [c], Frédéric Grandjean [k], Anne-Kristel Bittebiere [l], Maud Mouchet [m], François Massol [n]

[a] University of Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] - UMR 6553, Rennes, France
[b] Institut Universitaire de France, 1 rue Descartes, 75231 Paris Cedex 05, France
[c] Institut Méditerranéen de Biodiversité et d'Écologie marine et continentale (IMBE), UMR Aix Marseille Université, Avignon Université, CNRS, IRD, France
[d] Institut de recherche pour la conservation des zones humides méditerranéennes Tour du Valat, Le Sambuc, 13200 Arles, France
[e] NGE-GUINTOLI, Saint-Etienne du Grès, Parc d'activités de Laurade – BP22, 13156 Tarascon Cedex, France
[f] Naturalia-Environnement, Ingénierie en écologie, 20 Rue Lawrence Durrell, 84140 Avignon, France
[g] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany
[h] School of Biological Sciences, Queen's University Belfast, BT9 5DL Belfast, United Kingdom
[i] Dipartimento di Scienze, Università degli Studi Roma Tre, Viale G. Marconi 446, 00146 Roma, Italy
[j] Université de Picardie Jules Verne, UMR 7058 CNRS EDYSAN, 1 rue des Louvels, 80037 Amiens Cedex 1, France
[k] Université de Poitiers, UMR CNRS 7267 EBI- Ecologie et Biologie des Interactions, équipe EES, 5 rue Albert Turpin, Bat B8-B35, TSA 51106, 86073 Poitiers Cedex 09, France
[l] Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR5023 LEHNA, F-69622 Villeurbanne, France
[m] UMR 7204 MNHN-SU-CNRS CESCO, CP135, 57 rue Cuvier, 75005 Paris, France
[n] Univ. Lille, CNRS, Inserm, CHU Lille, Institut Pasteur de Lille, U1019 - UMR 8204 - CIIL - Center for Infection and Immunity of Lille, F-59000 Lille, France

HIGHLIGHTS

- Biological invasions have become a growing threat affecting biodiversity.
- Links between functional diversity and biological invasion concepts are explored.
- Functional diversity indices are valuable tools for testing ecological hypotheses.
- Functional diversity indices can reveal unexpected effects incurred by alien species.
- Novel directions are proposed to advance functional diversity indices in this field.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Jay Gan

Keywords:
Functional traits
Invasiveness
Invasibility
Community-weighted trait mean
Diversity indices
Alien invasive species

ABSTRACT

Pioneering investigations on the effects of introduced populations on community structure, ecosystem functioning and services have focused on the effects of invaders on taxonomic diversity. However, taxonomic-based diversity metrics overlook the heterogeneity of species roles within and among communities. As the homogenizing effects of biological invasions on community and ecosystem processes can be subtle, they may require the use of functional diversity indices to be properly evidenced. Starting from the listing of major functional diversity indices, alongside the presentation of their strengths and limitations, we focus on studies pertaining to the effects of invasive species on native communities and recipient ecosystems using functional diversity indices. By doing so, we reveal that functional diversity of the recipient community may strongly vary at the onset of the invasion process, while it stabilizes at intermediate and high

* Corresponding author at: Université de Rennes 1, UMR CNRS 6553 EcoBio, 263 Avenue du Gal Leclerc, CS, 74205, 35042 Rennes Cedex, France.
E-mail address: david.renault@univ-rennes1.fr (D. Renault).

http://dx.doi.org/10.1016/j.scitotenv.2022.155102
Received 17 January 2022; Received in revised form 31 March 2022; Accepted 3 April 2022
Available online 8 April 2022

0048-9697/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

levels of invasion. As functional changes occurring during the lag phase of an invasion have been poorly investigated, we show that it is still unknown whether there are consistent changes in functional diversity metrics that could indicate the end of the lag phase. Thus, we recommend providing information on the invasion stage under consideration when computing functional diversity metrics. For the existing literature, it is also surprising that very few studies explored the functional difference between organisms from the recipient communities and invaders of the same trophic levels, or assessed the effects of non-native organism establishment into a non-analogue versus an analogue community. By providing valuable tools for obtaining in-depth diagnostics of community structure and functioning, functional diversity indices can be applied for timely implementation of restoration plans and improved conservation strategies. To conclude, our work provides a first synthetic guide for their use in hypothesis testing in invasion biology.

Contents

1. Introduction . . . 2
2. Diversity indices: which ones, why and how? . . . 3
2.1. Rationale for diversity approaches . . . 3
2.2. The variety of functional diversity indices . . . 5
2.3. Data and constraints on diversity indices . . . 5
2.4. Diversity partitioning . . . 5
2.5. Community-weighted trait means . . . 5
3. Functional structure, functional diversity and biological invasions . . . 7
3.1. Functional attributes of invasive and native organisms: how different are they? . . . 8
3.2. Functional diversity indices as measures of invasion effects on communities . . . 8
3.3. Functional diversity indices, invasion theories and ecosystem function . . . 9
3.3.1. Describing and predicting the biotic resistance and invasibility of native communities . . . 9
3.3.2. Understanding the co-occurrence and co-existence of native and invasive species . . . 10
3.3.3. Using functional diversity indices to better describe novel species combinations and changes in mutualistic interactions? . . . 12
3.3.4. Linking the effects of invasion to ecosystem properties . . . 12
3.4. Combining effects of environmental conditions and biological invasions on functional diversity . . . 12
3.5. Evaluating the effects of invasive species removal . . . 13
4. Perspectives . . . 14
4.1. From functional diversity to interaction diversity? A network perspective . . . 14
4.2. Driven by data: opportunities and constraints in the context of biological invasions . . . 15
4.3. Towards predictive or explanatory models of invader impacts? . . . 16
5. Conclusions . . . 16
CRediT authorship contribution statement . . . 16
Declaration of competing interest . . . 16
Acknowledgements . . . 16
Appendix A. Supplementary data . . . 17
References . . . 17

1. Introduction

Biological invasions are acknowledged as a primary threat to biodiversity and ecosystem functioning (MEA, 2005; CBD, 2016; Genovesi et al., 2017; Pyšek et al., 2020). Non-native species are considered invasive when they sustain self-replacing and growing populations over several life cycles, reach large population densities, and widely spread far from their site of introduction (Richardson et al., 2000). Invasive species frequently exert substantial impacts on native communities at all levels of biological organization (Hulme, 2007; Cucherousset and Olden, 2011; Vilà et al., 2011; Crystal-Ornelas and Lockwood, 2020). At fine scales, possible effects include modification of gene pools (Sax et al., 2007), reduction of the fitness and growth of native organisms (Jauni and Ramula, 2015), and local extinction of both native and non-native populations (Bellard et al., 2016; Blackburn et al., 2019). At larger scales, alteration of the structure, composition, diversity and biotic interactions of the recipient communities can be observed (Hejda et al., 2009; Jucker et al., 2013). Moreover, modifications of ecosystem functioning, such as pollination, soil parameters, nutrient availability, microbial activity, and interaction networks (Bjerknes et al., 2007; Jordan et al., 2008; Ehrenfeld, 2010; Geslin et al., 2017; Mollot et al., 2017) have also been reported.

The impacts of invasive species on native communities are typically assessed through changes in taxonomic diversity. Several studies have reported multiple invasion-induced modifications of biodiversity (Sax and Gaines, 2003; Gurevitch and Padilla, 2004; Jucker et al., 2013; Murphy and Romanuk, 2014; Mollot et al., 2017), although the direction of changes can differ according to the observational scale (Sax and Gaines, 2003; Powell et al., 2011, 2013; Tomasetto et al., 2019). Invasion research is often partitioned in terms of investigation scales, with studies being conducted at populational, community or ecosystem scales, over short periods and reserved to single invasive species (Crystal-Ornelas and Lockwood, 2020). Local species diversity can be decreased by invasion (Hejda et al., 2009), e.g. in coastal dune plant communities invaded by *Carpobrotus* sp. (Vilà et al., 2006; Santoro et al., 2012). Conversely, diversity can increase at local scales and decrease at larger scales, due to the local arrival of the non-native species and the regional extirpation of rare, vulnerable species (Sax and Gaines, 2003). Negative effects can also occur at both scales, as e.g. in the case of the invasion of *Quercus suber* stands by the maritime pine *Pinus pinaster* (Selvi et al., 2016).

While taxonomic diversity has remained prominently used for evaluating the effects of invasions on biodiversity, the use of phylogenetic information has been proposed to predict the identity of invaders and their potential impact. Indeed, the probability of success of introduced species often increases with phylogenetic relatedness with native species (Rejmánek, 1996 in Californian grasses, Lockwood et al., 2001 in other plants, Van Wilgen and Richardson, 2011 in North American animal groups) due to reduced likelihood of competitive interactions (Darwin's naturalization hypothesis; Darwin, 1859, Davies et al., 2011).

However, empirical studies linking phylogenetic relatedness with invasion spread and impacts have been less conclusive (Strauss et al., 2006; Schaefer et al., 2011; Park and Potter, 2015; Tan et al., 2015). Neither taxonomic nor phylogenetic diversity captures the ecological role of species within a community, and hence both have difficulties predicting the potential impacts of invasions.

Functional traits (i.e. species characteristics, usually measured at the individual scale, influencing organismal performance, sensu McGill et al., 2006, Violle et al., 2007) are being increasingly used to understand organism-environment interactions, as well as community structure and functioning (Laureto et al., 2015). The idea of focusing on the functional characteristics of invaders to disentangle invasion processes dates back to Elton (1958), who related plant invasion success with specific attributes known to promote invasiveness, such as high fecundity and dispersal abilities (Drenovsky et al., 2012). Recent works have combined functional traits with functional responses and abundances to investigate the invasive-native interactions at population scales (Dick et al., 2017; Dickey et al., 2020). Other studies have attempted to disentangle the links between invasiveness and interactions with biotic and abiotic features of the invaded environment (Pyšek and Richardson, 2007; Hulme and Bernard-Verdier, 2018b). The main mechanisms underpinning the successful establishment of non-native organisms outside their geographic range, such as limiting similarity and habitat filtering, have been scrutinized through functional trait approaches (Ordonez et al., 2010), while others have thoroughly compared the traits and phylogenies of native and non-native species to uncover the main features of invasiveness (Van Kleunen et al., 2010a, 2010b). Yet, contradictory findings have been obtained so far (Daehler, 2003; Pyšek and Richardson, 2007), either because traits were coarsely assessed (binary instead of quantified trait values) or because functional diversity was estimated as regards to individual traits (e.g. using the abundance-weighted average trait value of the community; Ordonez et al., 2010). The need for measuring the traits of all species in a community has been demonstrated by the fact that some indices (e.g. functional dispersion, functional richness and Rao's entropy) show consistently lower values when the number of considered species or measured traits is reduced, whilst others (for instance functional divergence and evenness) feature higher or lower values (Pakeman, 2014). For this reason, the use of multi-dimensional approaches, relying on multiple traits or synthetic measures, such as functional diversity (FD) indices, has been encouraged (Hulme and Bernard-Verdier, 2018b).

FD has various definitions in the literature, usually corresponding to '*the value of those species and organismal traits that influence ecosystem functioning*' (Mason et al., 2005; Mason and de Bello, 2013) or '*the value and range of functional traits of the organisms present in a given ecosystem*' (Diaz and Cabido, 2001). In practice, quantifying FD amounts to assessing a few indices that can reflect the distribution of species traits in a "trait space" (also coined "functional space"). Functional traits can reveal biotic interactions (e.g. by relating species location in trait space to those of their predators and prey, Ulmer et al., 2021) or the effects of the surrounding environment (e.g. by mapping differences in trait values between environments), and thus allow a more mechanistic approach to investigate changes in community composition and ecosystem functioning (Petchey and Gaston, 2006; Cadotte et al., 2011). As a result, FD indices have been increasingly used since the 2000s to describe and quantify the effects of global change on communities and ecosystems (Mouillot et al., 2013; Schmera et al., 2017). Here, we aim at (i) listing and describing the different functional metrics available, and reporting their connection with invasion; (ii) reviewing the main results pertaining to the effects of invasive species on native communities and recipient ecosystems obtained using FD indices, and provide recommendations regarding the FD indices that are best adapted for addressing the different facets of biological invasions; (iii) providing suggestions and guidelines for the use of FD indices along different stages of the invasion continuum. Finally, with the aim of further stimulating debate and research on this theme, we propose new avenues for the use of these indices to investigate biological invasions.

2. Diversity indices: which ones, why and how?

2.1. Rationale for diversity approaches

Taxonomic, phylogenetic, functional and interaction diversity indices use data on several species to gauge community properties (e.g. their spatial structure and temporal dynamics) in order to answer a variety of ecological questions (e.g. related to the quantification of ecosystem services) (Lavorel et al., 2013). They can also link ecosystem disturbances, such as invasions, with ecosystem processes (e.g. productivity, Tilman et al., 1997; decomposition, Kuebbing et al., 2018). There are several bases for diversity metrics. The most notable are taxonomy (taxonomic diversity, TD), phylogeny (phylogenetic diversity, PD), ecological functions (functional diversity, FD), and species interactions (interaction diversity, ID) (also see Supplementary Material 1 to go even further in the presentation and understanding of these indices).

Most studies on biological invasions have focused on TD, PD and FD, often neglecting ID altogether, since obtaining knowledge on non-native species interactions is time-consuming and requires sufficiently high species abundances to allow enough individual sampling. While TD and PD indices inform on community composition (see Tucker et al., 2017 for a review of phylogenetic indices), thus reporting extinctions occurring after species invasions, FD indices are essential to capture more subtle effects of invasions such as niche displacement (Chapuis et al., 2017). In the following, we will mostly focus on FD indices, but parallels with other diversity contexts will be evoked when necessary. In general, FD indices use data on each species to calculate and summarize properties at the community level. However, some other metrics can be computed for a single species, relative to the rest of the community (e.g. functional originality, Pavoine et al., 2005), and these metrics are not diversity indices *stricto* sensu. For the sake of completeness and simplicity, we will generally call all indices, including such species-centred metrics, using the broad term of FD indices in this review.

Approaches based on diversity indices are classically contrasted to two other types of descriptive statistical models: (i) multivariate regression approaches, which elucidate large amounts of multidimensional community data through reduction in the number of dimensions and projection onto multivariate explanatory variables (e.g. Legendre and Gauthier, 2014; Buckley et al., 2018); and (ii) classification approaches, which model community properties by making groups of similar species (e.g. phylogenies obtained from molecular data, or modules within networks of interacting species) (Supplementary Material 1). The three approaches (diversity indices, multivariate regressions, classification approaches) are descriptive insofar as they are not necessarily based on probabilistic models and can be inferred without reference to goodness-of-fit criteria. Yet, compared to these two other types of analyses, diversity-based approaches offer some advantages: they are inherently geared towards the partition of variation between spatial scales (i.e. using alpha, beta and gamma diversities); their dependence on rare traits or species can be changed by using different families of indices (Chao and Chiu, 2016); they can be interpreted more easily than principal axes from multivariate approaches or interaction modules; they are connected to the Hutchinsonian theory of ecological niches. Meanwhile, diversity-based approaches are not necessarily exclusive of multivariate regression approaches or classifications – when many functional traits are used, principal component analyses (PCA) or distance-based redundancy analysis (db-RDA) might help correct for statistical dependences between traits (Mason et al., 2007) and classifications could be made based on the clustering of species traits, e.g. using Gaussian mixture of experts models (Murphy and Murphy, 2020).

FD-based approaches are now well accepted and have a sound, intuitive ecological underpinning. Yet, the huge number of available indices can be a hindrance if the ability of indices to predict community or ecosystem changes is variable (Mouchet et al., 2010; Schleuter et al., 2010; Santini et al., 2017; Kuebbing et al., 2018). Choosing the right indices and knowing data requirements needed to compute them is thus essential for diversity-based approaches to community assessments (see the next two sections of this review for a discussion on that aspect, and see Tables 1 & 2 for a

Table 1
Functional diversity metrics, their relevance in the context of biological invasions, and related indicators (indices). For each indicator, we report whether species' abundance is considered or not in the computation of the related indicators (see column 'abundance included'). Also, we provide literature references for each indicator. Further technical details on the calculation of the most commonly used indicators are presented in Table 2.

Functional metric(s)	Description	Connection to invasion	Main indicators	Abundance included	References
Richness	(i) Amount of trait space occupied by functional units i.e. the range of values of a trait or the hypervolume defined by multiple functional traits. (ii) Number of functional units in functional groups	Invasion resistance is expected to increase with functional richness, but saturated communities might be prone to invasion by functionally-distinct invaders	FR_{Ci} - the range of values of one trait $ FRic - the convex hull volume occupied by the community functional volume $ FR_{Is} and FR_{Im} – uni and multidimensional distribution of attributes in the functional space FD - the sum of branch lengths relating all the functional units in the community on the functional dendrogram §	No	FR_{Ci} - Mason et al., 2005 FRic - Cornwell et al., 2006, Villéger et al. 2008 FR_{IS} and FR_{Im} - Schleuter et al., 2010 FD - Petchey and Gaston, 2002
Evenness	Regularity of the distribution of abundances in the functional space. Both functional units and their relative abundances have to be regularly distributed to maximise functional evenness	A low functional diversity of the native community might result from niche packing with potential niche availability for invaders. Unless this low functional evenness is driven by environmental filtering, in which case only invaders functionally similar to native species might be successful	FRO - regularity of the distribution of values of a given trait $ FEve - abundance weighted sum of the minimum spanning tree branch lengths £	Yes	FRO - Mouillot et al., 2005 FEve - Villéger et al. 2008
Divergence and dispersion	Scattering of functional units around the community centroid in the functional space. Functional divergence depicts the degree to which the distribution of abundances maximises the deviation from the mean trait values of the community (i.e. the degree to which more abundant functional units tend towards the extremes of its functional volume). Functional dispersion rather depicts the standard deviation of abundances to the gravity centre of the functional space. Related concept: phenotypic divergence	Whether the invader maximises or reduces divergence/dispersion should give insights on its generalist/specialist ability (but to be confronted to values of functional originality and specialisation). FDis may increase at early invasion stages if the invader extends the trait space in the invaded community	FD_{var} - logarithmic variance of the value distribution of a given trait $ FD_Q or FEnt - variance of abundance-weighted functional distances between functional units (Rao's quadratic entropy) £ FDiv - abundance-weighted deviation from the average distance of functional units to the centre of gravity of the functional space £ FDis - mean abundance-weighted distances of functional units to the centre of gravity of the functional space £	Yes	FD_{var} - Mason et al., 2005 FD_Q - FEnt - Rao, 1982, Botta-Dukat 2005 FDiv - Villéger et al. 2008 FDis- Laliberté et al., 2010
Overlap	Amount of the trait space (also named functional niche when related to a single species) shared by two or more functional units	Functional overlap between natives and invasives is bound to decrease after invasion (niche displacement)	Overlap between trait probability density functions $ FOve - overlap of hypervolumes (convex hull volume) $	No	Overlap - Blonder et al., 2014, Carmona et al., 2016 FOve - Villéger et al., 2013
Identity	Position of a species or a group of organisms in the functional space	The functional identity of invaders can be compared with the functional identity of native species to detect potential functional overlap and redundancy	CWM - community-level abundance-weighted means of traits or proportion of modalities of categorical traits $ FIde - average position of the functional unit in functional space (i.e. its average position along each functional axis) $	Depends on the index	CWM - Ackerly et al., 2002, Garnier et al., 2004 FIde - Toussaint et al., 2018
Originality and uniqueness	Position of the functional units in the functional space relative to the rest of the community. Functional originality indicates the rarity of a functional unit's trait values within a community, which depends on both the uniqueness and the average distance to all others. Uniqueness is the number of functional attributes that are not shared by other functional units in the community and may be used to complement functional identity. Related concept: distinctiveness	A community with a high degree of originality or uniqueness might occupy all available niches, leaving few opportunities for colonization	FOri - euclidean distance to gravity centre of the species pool (hypervolume) £ NN - distance to the nearest neighbour in the functional space (dendrogram) § Uniqueness - euclidean distance to the nearest neighbour in the functional space £	No	FOri - Mouillot et al., 2013 NN - Pavoine et al., 2005, Pavoine et al., 2017
Specialisation	Variance in species' impact (Eltonian specialisation) or performance (Grinellian specialisation) on the ecosystem. Broadly, it reflects the width of a species' functional niche	The level of specialisation in the community may result from contrasting forcing (i.e. habitat heterogeneity or disturbance). Heterogeneous habitats with various resources might be favourable for invaders, especially generalist ones. Stressful environments might favour specialist species, and so invaders should have a similar specialisation to establish	SSI - coefficient of variation of species' density or abundance across habitats $ FSpe - (abundance-weighted) mean distance between a given species and the average position the assemblage £	Depends on the index	SSI - Julliard et al., 2006 FSpe - Mouillot et al., 2013

Table 1 (*continued*)

Functional metric(s)	Description	Connection to invasion	Main indicators	Abundance included	References
Redundancy	When several functional units have the same function or functional trait values in the community. Functional redundancy is also related to the number of species in a given functional group	High functional redundancy in the native community may result from strong environmental filtering. Therefore, invasions may be successful if the invader has similar functional traits values to native species	FR_R - difference between Simpson's index diversity and Rao's quadratic entropy £ R or FRed - complement of functional uniqueness £ FRed - average overlap in trait probability density of species in the community (or regional pool) $	Depends on the index	FR_R - de Bello et al., 2007, Pillar et al., 2013 R or FRed- Ricotta et al., 2016 FRed - Carmona et al., 2016

$: attribute-based index; £: distance-based index; §: dendrogram-based index.

presentation of the different functional diversity metrics). Mason et al. (2005) first introduced the idea of multiple indices, each aimed at qualifying a particular aspect of FD – initially comprising functional richness, evenness and divergence. Among these indices, some can be called "intensive" and others "extensive" (borrowing terminology from thermodynamics), based on their dependence on the taxonomic diversity of the community: extensive indices, e.g. functional richness, necessarily increase with species richness; intensive indices, on the contrary, are independent from species richness (see e.g. functional evenness measures in Mouchet et al., 2010, Schleuter et al., 2010) and can thus be compared between communities constituted by a different number of species.

2.2. The variety of functional diversity indices

FD indices can be clustered into three main types: (i) attribute-based indices, which make use of species positions in trait space to compute either centroids (e.g. community-weighted means of traits Ackerly et al., 2002, Garnier et al., 2004) or other statistics based on the distribution of trait values (Mason et al., 2005); (ii) distance-based indices, which rely on pairwise distances among species in trait space (e.g. Rao's quadratic entropy, Rao, 1982, Botta-Dukát, 2005); (iii) dendrogram-based indices, calculated using branch lengths on the functional dendrogram built from species' trait values (Petchey and Gaston, 2002; Podani and Schmera, 2006) (Supplementary Material 1).

In the context of biological invasions, it is suggested that species-level indices can complement the aforementioned community-level indices by focusing on the functional profile of the invader and its contribution to diversity. For instance, the functional identity of the invader, estimated following Toussaint et al. (2018), represents its average position in the functional space (i.e. average position on each PCA axis; Ulmer et al., 2021). The range of its habitat preferences can be estimated using the specialisation index from Julliard et al. (2006), later averaged at the community-level by Clavel et al. (2011). Finally, its redundancy to native species can be investigated with indices of niche overlap (Blonder et al., 2014; Swanson et al., 2015; Blonder, 2018). These approaches can be generalized at the community-level (Villéger et al., 2013; Carmona et al., 2016; Zhao et al., 2019).

2.3. Data and constraints on diversity indices

A crucial aspect of diversity indices is their dependence on species-specific data, and on the quality of the measurements (Jarzyna and Jetz, 2016). In the case of FD indices (Table 1, see also Mouchet et al., 2010, Schleuter et al., 2010, Cadotte et al., 2011, Gagic et al., 2015, Schmera et al., 2017), while data for a single trait (or an average value of the trait for each species) are necessary for the computation of FD, more trait data are necessary if we are to inform the multifunctionality of a species. Regarding the number of functional traits required for a robust estimation of functional diversity, there are no rules except for those relative to technical constraints (Supplementary Material 1).

In the context of species invasions, many conclusions stemming from the analysis of diversity indices depend on data provenance. FD indices are particularly sensitive to data provenance. For instance, comparing FD pre- and post-invasion will evince cases of niche displacement (Chapuis et al., 2017; Wong et al., 2019) if species traits are only measured where the invasion is occurring. Similarly, the post-invasion changes of invasive species FD can only be assessed if such data are actually measured in the field. An increasing number of studies is making use of trait values stored in databases (e.g. TRY, Kattge et al., 2020, BETSI, Pey et al., 2014, FishBase, Froese and Pauly, 2021). As with any ecological data, care should be taken when using traits measured in a different ecosystem, or at a different times or seasons, as these trait values might not be representative of the actual values in the studied assemblage, or in the studied geographic / climatic region. This is especially true in the case of biological invasions, where biological and ecological characteristics of the invaders are susceptible to change rapidly during the invasion process (Leishman et al., 2014; Vandepitte et al., 2014), and subject to the range of context-dependencies that mediate invasion dynamics (Thomsen et al., 2011; Ricciardi et al., 2013). Therefore, using trait values from the native range of invaders might not be a good surrogate of their trait values in the invaded range.

2.4. Diversity partitioning

Diversity studies classically compare average community diversities and their aggregated metrics at large spatial or temporal scales, i.e. alpha, beta and gamma diversities (Lande, 1996; de Bello et al., 2010; Chao et al., 2012; Villéger et al., 2013; Ohlmann et al., 2019) (Supplementary Materials 2). Yet, very few studies have placed FD changes in a scale- or time-dependent context (Jarzyna and Jetz, 2018), and only two concern invasive species. The recent invasion of ant communities in Hong Kong by the fire ant *Solenopsis invicta* induced only a marginal decline in both species and functional richness indices of invaded communities, but noticeable changes in the taxonomic and functional composition (Wong et al., 2019). The decline in species and functional richness may be limited in the first stages of the invasion, and then intensify as the invader triggers species extirpation and/or homogenization. Based on (Wong et al., 2019), invasion seems to first alter community functional identities through a high turnover in trait distributions, ending up with more functionally homogeneous ant communities. By monitoring invasions over two centuries in a river system, Haubrock et al. (2021) found FD of native species to decrease over time, and that of invasive species to increase concurrently, causing an almost complete turnover in niche space. That study suggested increased competition, as well as environmental disturbances such as changes in hydromorphology and an increase in pollution, as drivers of native species extirpation (Haubrock et al., 2021). In light of this limited literature, we suggest that predicting how FD indices could respond to invasion processes over time remains a key challenge to be tested with robust datasets from both mesocosm and field studies.

2.5. Community-weighted trait means

Functional heterogeneity within a community, calculated with the FD indices described above, is very often complemented with the average functional position of the considered community in niche space. To that aim,

Table 2
Most commonly used functional diversity metrics. For each indicator, the table reports: i) its formula; ii) whether the index is intensive (I, responds to species richness) or extensive (E, does not depend on species richness); iii) the known correlations with other indices; iv) expectations and limitations associated with the use of the index (note here that some of the presented indices have not been benchmarked yet due to the lack of studies analysing their redundancy and functioning under different ecological contexts; but see Laliberté et al., 2010; Mammola et al., 2021; Mouchet et al., 2010; Schleuter et al., 2010; Galland et al., 2020 and associated references).

Metric(s)	Formula	I/E	Correlated to	Expectations and limitations	Reference(s)
Functional identity					
Community-weighted mean (CWM)	$CWM = \sum_{i=1}^{S} p_i x_i$	–	–	By definition, CWM is driven by the attributes (trait values) of most abundant species. CWM is a one-dimensional metric.	Ackerly et al. (2002); Garnier et al. (2004)
Functional richness					
Functional Range FR_{Ci}	$FR_{Ci} = \frac{SF_{ci}}{R_x}$ with SF_{ci} and R_c being, respectively, the niche space filled by the species within the community i and the absolute range of the trait x	E	FD_{var}	Reduction of FR_R when species are removed at the edge of the community. Individual variability or gaps are not considered. FR_R is a one-dimensional metric.	Mason et al. (2005)
Functional Richness FR_{Im}	$FR_{Im} = \int_{s \in Si} max\,(f_s(X))dX$ with f_s a normal density function of the trait attributes X in the community i	I	–	$FRic_{Im}$ is computation-intensive, and it requires information on intra- specific trait variation.	Schleuter et al. (2010)
Functional Richness FRic	FRic equals the volume inside the minimum convex hull that encloses all species in functional space	I	FD, to a lesser extent FD_Q and FDiv	The number of measured traits must be lower than species richness. This metric does not consider gaps within the functional space (hull volume), i.e. only vertices are accounted for in the calculation of FRic.	Cornwell et al. (2006); Villéger et al. (2008)
Functional Diversity FD	$FD = i'.h2$ with i' being the branch presence/absence row vector and $h2$ the transposed branch length vector of the functional tree (dendrogram)	I	FRic	Getting a reliable functional dendrogram may take time (see Mouchet et al., 2008 and Mérigot et al., 2010). FD is often used when the conditions are not met to estimate FRic (number of species > number of traits) or to be compared with Faith's PD (phylogenetic diversity) index.	Petchey and Gaston (2002)
Functional evenness					
Functional Evenness FEve	$FEve = \frac{\sum_{l=1}^{S-1} min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1-\frac{1}{S-1}}$ with the partial weighted evenness $PEW_l = \frac{\frac{d(i,j)}{w_i+w_j}}{\sum_{l=1}^{S-1} 1 W_l}$	E	–	By construction, FEve ranges from 0 to 1.	Villéger et al. (2008)
Functional divergence					
Functional Divergence FDiv	$FDiv = \frac{\Delta d + dG}{\Delta \lvert d \rvert + dG}$ with Δd, $\Delta \mid d \mid$ and dG being, respectively, the sum of abundance-weighted deviances, the absolute sum of abundance-weighted deviances from the centre of gravity G, and the average distance of the S species to G	E	FD_Q, and to a lesser extent FRic		Villéger et al. (2008)
Functional Divergence FD_{var}	$FD_{var} = \frac{2}{\pi}\, arctan\left[5 \times \sum_{i=1}^{N}\left[\left(ln\, x_i - ln\underline{x}\right) 2 \bullet p_i\right]\right]$ where p_i is the proportional abundance of the i^{th} attribute category	E	FR_{ci}	The metric does not accept 0-values and is a one-dimensional metric.	Mason et al. (2005)
Rao's Quadratic Entropy FD_Q	$FD_Q = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij} p_i p_j$	E	FDiv and FDis, and to a lesser FRic	FD_Q is sensitive to the number of species at low levels of S, but not when S is intermediate or high.	Rao (1982); Botta-Dukát (2005)
Functional differentiation / redundancy / specialisation					
Functional Originality FOri	$FOri = \underline{dNN}$ with dNN being the average distance between a species and its nearest neighbour NN in the functional spaces	–	–	FOri is calculated for each species and can be averaged at the community level.	Mouillot et al. (2013)
Functional Specialisation FSpe	FSpe is the average Euclidean distance between a species and the average position of all other species in the functional space	–	–	FSpe is calculated for each species and can be averaged at the community level.	
Functional Redundancy FRed	$FRed = 1 - U$ *with* $U = \frac{FD_Q}{1-D}$, U being an estimate of functional uniqueness, and D the Simpson's dominance index	E	FD_Q		Ricotta et al. (2016)
Functional Dispersion FDis	$FDis = \frac{\sum p_i dG_i}{\sum p_i}$ (dG is defined for FDiv)	E	FD_Q		Laliberté and Legendre (2010)

S: species richness, p: species' abundance or biomass (often relative), d: distance.
Non-exhaustive list of R packages to compute the listed indices: FD (Laliberté et al., 2014); adiv (Pavoine, 2020); vegan (Oksanen et al., 2020); ade4 (Dray and Dufour, 2007); cati (Taudiere and Violle, 2016); TPD (Carmona et al., 2019); mFD (Magneville et al., 2022); betapart (Baselga et al., 2022); BAT (Cardoso et al., 2021). See de Bello et al. (2021) for a hands-on guide on how to compute most of the following indices. Note that indices and R packages are continuously developed and, therefore, this list should be updated in the coming years.

community-weighted means (CWM) (Table 1), i.e. average trait values weighted by the abundance of each species composing the community, are employed (Ackerly et al., 2002; Garnier et al., 2004; Domínguez et al., 2012) (Supplementary Material 1). CWM thus describes the dominant functional position of the considered community and further allow generation of assumptions on ecosystem properties. The use of CWM may be particularly appropriate for assessing the effects of an invader on the recipient community as it synthetically summarizes community properties. However, the use of CWM is of limited value when aiming to primarily consider rare species and their traits, given that their characteristics are subsumed by those of more dominant taxa.

The establishment of a non-native species in a community can lead to a modification of the CWM due to: (i) the non-native species having a trait value very different from those of the native species; (ii) the trait of the

non-native being only slightly different, but its abundance growing to dominate the community; or (iii) the native species changing their trait values in response to species invasion. Importantly, CWMs are usually not used to describe the invader trait value in comparison to the traits of native species from the community (i.e. the above-mentioned case (i)) because FD indices already successfully distinguish and characterize functional outliers. Conversely, cases (ii) and (iii) above, which concern already well-established non-native organisms and niche displacement, respectively, represent two scenarios of great interest for invasion studies. CWM can be computed for those species whose abundances sum up to at least 80% of the studied community abundance, since trait data are generally not available for all occurring species (Pakeman and Quested, 2007). Yet, even if the addition of more species with trait data does not affect the accuracy of CWM, Borgy et al. (2017) reported the importance of increasing the proportion of species in the calculation over 80%, as it reduces potential biases on the computed CWM (Májeková et al., 2016).

3. Functional structure, functional diversity and biological invasions

The use of FD indices to assess the ecological effects of invasions should strongly enhance our understanding of invasion dynamics, as several hypotheses can be tested (Fig. 1). For instance, an invasive species can drive towards extinction native species with similar trait values (Fig. 1f), hence increasing the functional divergence of the community without any

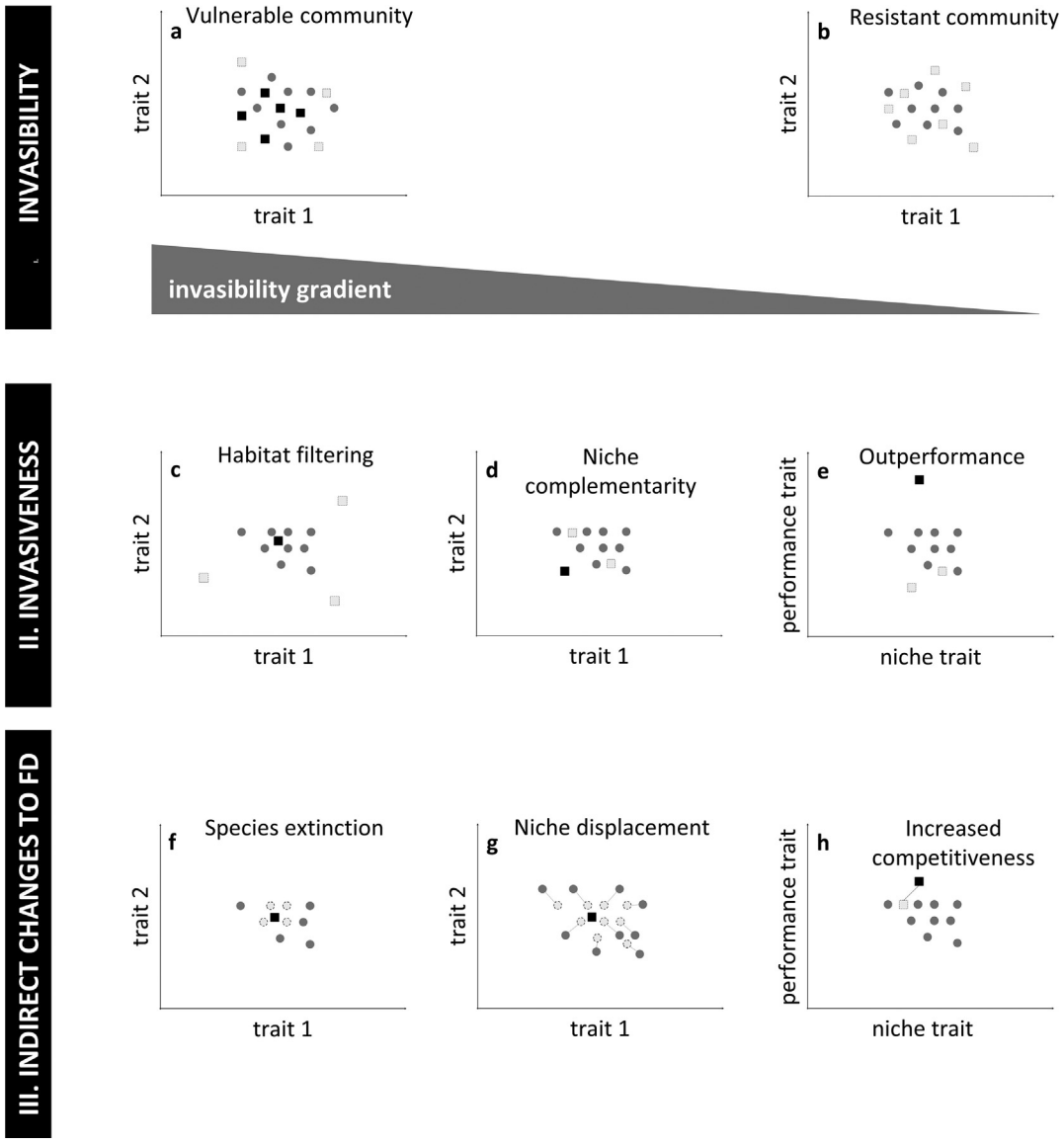


Fig. 1. Schematic representations of functional trait distributions and their change in response to invasion, focusing on (i) community invasibility (panels a-b), (ii) non-native invasiveness (panels c-e), and (iii) indirect changes to functional diversity due to invasions (panels f-h).
Persistent native species are filled in grey, successful invaders are black-filled squares. Natives and non-natives that have gone extinct are represented using dotted circles or squares, respectively.
Invasibility: (a) more vulnerable or (b) more resistant communities are contrasted based on which non-natives (with successful trait combinations) could invade or would fail to do so (solid black squares versus dotted squares).
Invasiveness: The invasiveness of non-natives can depend on their trait values. They can be filtered out (dotted squares) or can invade (filled black squares) depending (c) on the match of their traits with environmental requirements, or (d) with those of natives, or (e) depending on their trait values for performance traits only.
Indirect changes to functional diversity: Functional diversity metrics can also vary during the invasion as a consequence of non-native establishment, e.g. (f) due to native species extinctions (dotted circles), (g) native species trait shifts, or (h) the rapid evolution of non-native traits in response to the absence of predators and pathogens (i.e. enemies, EICA hypothesis) in the invaded range or to the selective pressures induced by the native community on performance-related traits. Finally, functional diversity metrics can vary following ecological restoration via the removal of invasive species (i) (the case of secondary invasion is not depicted).

detectable effect on functional evenness or richness. If some of the species traits are allowed enough time to adapt, either through plasticity or genetic adaptation, the arrival of an invader can even increase functional divergence further through niche displacement (Fig. 1g). One can also use the functional space as an indicator of ecosystem invasibility (Fig. 1a, b). In this respect, greater functional evenness can promote resistance against invasion, or buffer species invasiveness (Fig. 1c-e), whereas functional originality (see Tables 1 and 2 and Pavoine et al., 2017 for a definition) might promote invasiveness under the niche complementarity hypothesis.

3.1. Functional attributes of invasive and native organisms: how different are they?

Overall, it has been acknowledged that invasive species frequently feature a set of functional traits, mainly related to competitiveness (e.g. growth rate, morphology, aggressiveness, or dispersal ability), which promotes their establishment and persistence outside their native ranges (Pyšek and Richardson, 2007; Ordonez et al., 2010; Van Kleunen et al., 2010b; Leffler et al., 2014; Ordonez, 2014). In this regard, studies based on single-trait comparisons revealed high functional dissimilarity between native and non-native fish species (Matsuzaki et al., 2013; Matsuzaki and Kadoya, 2015). Similarly, van Kleunen et al. (2010b) found differences in the values of invasiveness-related plant traits (e.g. leaf area allocation, shoot allocation, growth rate) when comparing invasive, non-invasive and native species. The analysis of the functional divergence between invaders and natives represents a valuable tool for the identification of habitats which are more vulnerable to invasion, and for estimating the magnitude of invasion impacts (Gallien and Carboni, 2017; Hulme and Bernard-Verdier, 2018b; Wong et al., 2019).

The functional profiles of invasive and native organisms have also been compared using multi-trait approaches, and notably multidimensional metrics. For instance, Klonner et al. (2016) worked with Austrian terrestrial vascular plants, and used functional diversity indices (Functional richness: FRic; Functional dispersion: FDis, Table 1) to examine if invasive plants exhibit distinct trait profiles as compared with native plants in a multidimensional trait space. The distinction of native and invasive plants was improved when working with multiple traits as compared with single-trait analyses, but did not fully explain invasion success (Klonner et al., 2016). Likewise, Ordonez et al. (2010) computed FDiv and FRic metrics on 4473 plant species and reported that invasive and co-occurring native plant species differed when traits were considered separately; yet, they also suggested that multi-traits approaches considerably improve our understanding of invasion success. In animals, Escoriza and Ruhí (2016) tested the functional originality between source and recipient communities of two worldwide invasive frogs (the bullfrog *Lithobates catesbeianus* and the cane toad *Rhinella marina*). These authors found that both invasive species were functionally distant from their respective recipient communities. In both plants and animals, the studies from Ordonez et al. (2010) and Escoriza and Ruhí (2016) support the idea that high functional distance between invasive and native species contributes to a higher invasion success.

The identification of key traits discriminating invasive and native species is, however, highly context-dependent (Hulme and Bernard-Verdier, 2018a). A certain degree of complexity arises from the fact that species invasiveness, along with functional differences between invasive and native species, is simultaneously affected by a wide range of factors, whose influence is not always consistent among varying temporal contexts, e.g. invasion stages/phases along the introduction-naturalization-invasion continuum (Richardson and Pyšek, 2012; Divíšek et al., 2018), or spatial scales, from local to regional (Dietz and Edwards, 2006; Fridley et al., 2007; Carboni et al., 2013; Gallien and Carboni, 2017; Catford et al., 2019). In this regard, Thompson & Davis et al. (2011) concluded that the most invasive plant species are those having traits favouring their persistence both inside and outside their native range, but that these traits are similar to those of the most successful plants worldwide regardless of their status (invasive or native). As a supporting example, we note invasive species thriving in low-resource environments, whose sets of functional traits do not substantially diverge from those of "successful" native species (Leffler et al., 2014; Funk et al., 2016). If the multidimensional variability in trait space is higher in invasive organisms (i.e. if there is a higher intraspecific variability of trait expression and among ecological contexts), we can expect that this should be partially supported by a higher degree of phenotypic plasticity. In turn, this means that the effects of non-native organisms on the FD of the invaded community will be highly context-dependent. Our ability to disentangle the effects of environmental filters from the effects of biological traits in the regulation of native and invasive species coexistence is thus crucial for improving our understanding of invasion success and its impact on recipient communities.

3.2. Functional diversity indices as measures of invasion effects on communities

Non-native species can have negative or positive effects on the functional diversity of the recipient community, or even can have no detectable effect. In this regard, FD indices are being increasingly used for gaining deeper insights into the effects of non-native organisms on the structure and functioning of communities. Indeed, by combining information on taxonomic and functional diversities, it is possible to better understand biotic changes associated with invasions. As a result, a range of studies has considered the effects of invaders on both TD and FD indices to examine if these metrics would exhibit similar changing patterns during invasion. For instance, both TD and FD of recipient plant communities increased during the early stages of invasion by the non-native plant *Lantana camara*, most likely because the addition of this species extended the trait space of the invaded community (Mandle and Ticktin, 2015). Conversely, taxonomic and functional richness decreased drastically in the presence of the invaders *Carpobrotus* sp. or *Humulus japonicus*, as these species had high competitive exclusion abilities (respectively Castro-Díez et al., 2016, Fried et al., 2019). Matsuzaki et al. (2016) observed that multiple invasions of lakes by piscivore fish resulted in a substantial decrease in taxonomic and functional diversities, ending in the quasi-extirpation of some native fish encompassing specific features, i.e. fish having small body size, low fecundity, and narrow diet breadth.

While the above-mentioned examples revealed consistent changing patterns for TD and FD indices, other investigations have resulted in divergent conclusions. For instance, Schirmel and Buchholz (2013) observed greater changes in functional dispersion (FDis) (Tables 1 & 2) than in taxonomic diversity in dune spider communities invaded by the moss *Campylopus introflexus*. Their results also suggested that different spider species may colonize the community after moss invasion, adding new traits to the system, while spider species sharing similar traits may disappear. Toussaint et al. (2018) found that functional richness (FRic) (Tables 1 & 2) increases 10-fold more than taxonomic diversity, revealing the drastic FD implications of functional changes in freshwater fish assemblages alongside the introduction of invasive fish species over the last two centuries. The sensitivity of the computed metrics may also highly depend on the observational scale of the study. For instance, TD can be more sensitive to invasion than FD metrics when observations are conducted at the landscape scale (Fried et al., 2019). In particular, these authors observed greater changes in TD (γ-diversity) than in functional richness (FRic) in plant communities invaded by the Japanese hop *Humulus japonicus*. Yet, native species coexisting with the invader can still cover most of the functional space (Fried et al., 2019). In other invaded areas, the decrease of FD, as measured with functional divergence (FDiv) (Tables 1 & 2), has often been reported and reveals a functional homogenization of the invaded communities (Castro-Díez et al., 2016; Wong et al., 2019).

The selection of functional indices that would detect the effects of invaders on the recipient community should be determined according to the invasion stage. At early invasion stages, or more generally, when the non-native species are not yet dominant in the invaded community (e.g. due to invasion debt, Essl et al., 2011), the functional dispersion index (FDis) within community (Staab et al., 2015; Haubrock et al., 2021) appears particularly appropriate. FDis reports the mean distance of all functional traits to the centroid of the community, and changes to this

dispersion in the late stages of invasions can give insights into the generalist or specialist nature of invaders (i.e. functional originality). FDis is expected to increase at early invasion stages when invaders extend the trait space. In sum, using FDis for delineating the effects of biological invasions, in complement to FDiv and FOri, can be particularly useful for estimating the divergence between the traits of the non-native(s) and organisms of the invaded community.

At later invasion stages, when invaders become dominant, analyses of CWM values may be more suitable for the assessment of the impacts of non-native organisms on communities. Kimball et al. (2016) found that changes in CWM values after environmental perturbations depended on the studied ecological context (grassland versus coastal sage shrub). Using this metric, mixed conclusions have been reported when assessing the effects of invaders on communities, and several studies have even failed to quantify differences in the CWM of non-invaded versus invaded communities. For instance, Lee et al. (2017) found that CWM measured from a reference (non-invaded) community was not a good predictor when assessing potential effects of a non-native plant on N cycling. Even if that meta-analysis excluded some traits relevant to N-cycling for the computation of the reference non-invaded CWM, the use of reference CWM is generally less efficient in predicting and explaining variability of the effects of invasion compared to other indices (Májeková et al., 2016). When exotic species have trait values similar to those of natives, it is however worth mentioning that both CWM and FD indices have evidenced, in a complementary fashion, the effects of the invaders in a litter mixture decomposition experiment (Finerty et al., 2016).

Most often, the simultaneous/combined use of several FD indices is essential to accurately capture the modifications of the structure and functioning of communities undergoing invasion (Colin et al., 2018; Toussaint et al., 2018; Wong et al., 2019). As an example, the invasive fire ant *Solenopsis invicta* does not change TD, nor functional richness of native ant communities, while altering their functional identity and leading to increased functional homogenization (FDiv, Rao, FRed) (Wong et al., 2019). Shuai et al. (2018) showed that the TD of fish communities does not change with invasion intensity, whereas functional richness decreases and functional divergence and specialisation increase; the use of these different metrics allowed concluding that most native species are replaced by non-native species with different functional traits, which may ultimately affect ecosystem stability. In some cases, the use of different metrics may allow for identifying the main factors driving the invasion success, as in the study conducted by Gooden and French (2015). These authors concluded that the effect of the buffalo grass (*Stenotaphrum secundatum*) invasion on plant community productivity depends on the functional identity of the invaded community. Specifically, plants with root networks differing from those of *S. secundatum* are less affected by the invader, and more likely to compete and resist invasion. It is worth mentioning that this finding is in line with the earlier work of Emery and Gross (2007), who also found that the identity of the dominant plant species of the community drives the chances of establishment success of new arrivals.

The increased use of FD indices in invasion studies over the past few years has allowed a better understanding and description of the considerable alterations of the functional structure of recipient communities (FRic, FEve, FDiv, FDis, FR, Tables 1 & 2) (Schirmel and Buchholz, 2013; Castro-Díez et al., 2016; Colin et al., 2018; Fried et al., 2019; Wong et al., 2019). Real-time adjustments of trait values are often observed in living organisms to keep biological performance as high as possible; this makes trait-based approaches more sensitive to changes in environmental conditions, including biological invasions, than TD or many other biological indices (Mirzaie et al., 2013; Thukral, 2017). In this line, the study of Colin et al. (2018) first revealed the importance of FD indices as valuable metrics for assessing the mechanisms through which invasion processes reshaped the structure of a species-poor fish assemblage. Those authors demonstrated that functional specialisation, functional originality, and functional entropy best describe the changes occurring during fish invasion. Functional originality is strongly associated with non-native fish biomass (Colin et al., 2018). One of the caveats of originality is the selection of the index that will be used for subsequently calculating functional originality. The uniqueness of a trait can be used as a selection criterion, but may be too restrictive, while the mean distance to the average value of the trait of all other species represents a potentially more balanced alternative (also see the review Kondratyeva et al., 2019 for a discussion on originality and rarity and their associated indices). Importantly, the nature of co-existing native species also drives the probability of naturalization of non-native species, with the number of native species in a genus apparently favouring the process (Diez et al., 2008). Pellock et al. (2013) additionally noted the importance of competition and resource opportunities for non-native species which are significantly higher at early stages of invasion than at later ones. In conclusion, as factors controlling invasibility of the community may also change throughout the invasion process, and cause a temporal shift in the diversity–invasibility relationship (Clark and Johnston, 2011), the nature of the FD indices selected in a study should be driven by the invasion stage under consideration.

3.3. Functional diversity indices, invasion theories and ecosystem function

3.3.1. Describing and predicting the biotic resistance and invasibility of native communities

The use of FD indices has allowed identifying community processes and, in particular, biotic interactions that may drive the rate of invasion (Dyderski and Jagodziński, 2019). Biotic resistance, i.e. the ability of a species assemblage to limit the recruitment or invasion of other species from the global pool (Levine et al., 2004), may be mediated by TD and FD of recipient communities (Elton, 1958; Feng et al., 2019). Using experimental approaches, establishment success of newly arriving non-native organisms has been negatively correlated to initial TD, suggesting that species-rich sites are more resistant to invasion at the local scale (Tilman, 1997; Byun et al., 2013; Connolly et al., 2018). In addition, Hooper and Dukes (2010) suggested that more functionally diverse communities are less susceptible to invasion (Fig. 2). The majority of studies conclude that the use of FD, more than the number of species per se, better explains the increased resistance of communities to invasion (Fargione et al., 2003; Fargione and Tilman, 2005; Hooper and Dukes, 2010; Larson et al., 2013; Wei et al., 2015).

At the ecosystem scale, however, different patterns can emerge in the causal relationships between invasion success and FD. By considering multiple organism traits, FD can be used as a good predictor of the invasibility of communities, and of the main mechanisms shaping the degree of invasibility (Catford et al., 2019; Feng et al., 2019). Despite the low number of illustrated cases in the literature, a high FD of native communities can contrastingly increase the invasion success of non-native species, and this "native turncoat" effect apparently increases with the number of resources produced by native species in the resident community (Fig. 2-e). Accordingly, it is important to distinguish between intra-community and intra-ecosystem interactions in the context of invasion success, whereby high FD could be more likely to limit invasion success at the community scale (i.e. limit invasion by competing species), but conversely could promote invasion at the ecosystem scale (i.e. promote invasion of species interacting through modes other than competition, e.g. predation). This is the case of the invasive fruit fly *Drosophila suzukii*, for which polyphagy enables benefitting from a high diversity of fruit resources (functional types of fruits based on their anatomy, colours, shapes, skin types, size) (Poyet et al., 2015). Invasive pollinators also benefit from the native diversity in floral resources (Roubik and Villanueva-Gutiérrez, 2009). Savage et al. (2009) showed that an increasing dominance of plants with nectar is associated with increased abundances of an invasive ant and reduced native ant richness. Earlier work in coastal marine habitats showed that the identity of functional groups is more important than FRic in determining the ability of macro-algal communities to resist invasion (Arenas et al., 2006). Numerous works confirmed this observation in various contexts and taxonomic groups (Wardle, 2001; Flombaum et al., 2017; Mason et al., 2017), showing that FRic alone sometimes fails to explain invasion success. In some cases, both functional group identity and diversity of resident communities are

good indicators of biotic resistance to invasion (Byun et al., 2013); in other cases, the dominance of specific functional groups mainly explains community resistance (Longo et al., 2013) (Fig. 2-b). However, as the use of FD indices in an invasion context is very recent, it will require further study and synthesis before it is possible to obtain a complete overview of the indices that best represent the level of community resistance to invasion.

3.3.2. Understanding the co-occurrence and co-existence of native and invasive species

The competition between native and invasive organisms, and the effects of invaders on the community, may be lowered when populations occupy different ecological, spatial and temporal niches (MacDougall et al., 2009; Fried et al., 2019) (Fig. 2-d). In these circumstances, native and invasive species co-occur (i.e., do not exploit the same resources) rather than coexist (i.e., exploit the same resources) in different microhabitats of the same community or ecosystem. A high functional dissimilarity (Pavoine and Ricotta, 2019) between the species composing the community and the invader could manifest in reduced direct effects of the invader, as this would reduce the level of competitive interactions (Ordonez et al., 2010; Pereira et al., 2017). In particular, competition should be reduced in communities having higher functional specialisation (FSpe) and divergence (FDiv) values (Tables 1 & 2), and we may expect lower effects of invasive species on the FD of these communities. The results from Fried et al. (2019) support this assumption, with traits of resident plant species that persist in invaded communities being distinct from those of invaders. More recently, McGrannachan and McGeoch (2019) found evidence for trait-divergence along an invasion gradient, characterized by an increase in trait functional diversity with invasion level.

Invaders with niches distinct from those of native species should thus co-occur with little impact on local FD (Fig. 2-d). For example, resident species that use a different temporal niche can co-occur with the invader (Hejda and de Bello, 2013; Fried et al., 2019). Phenological differences in

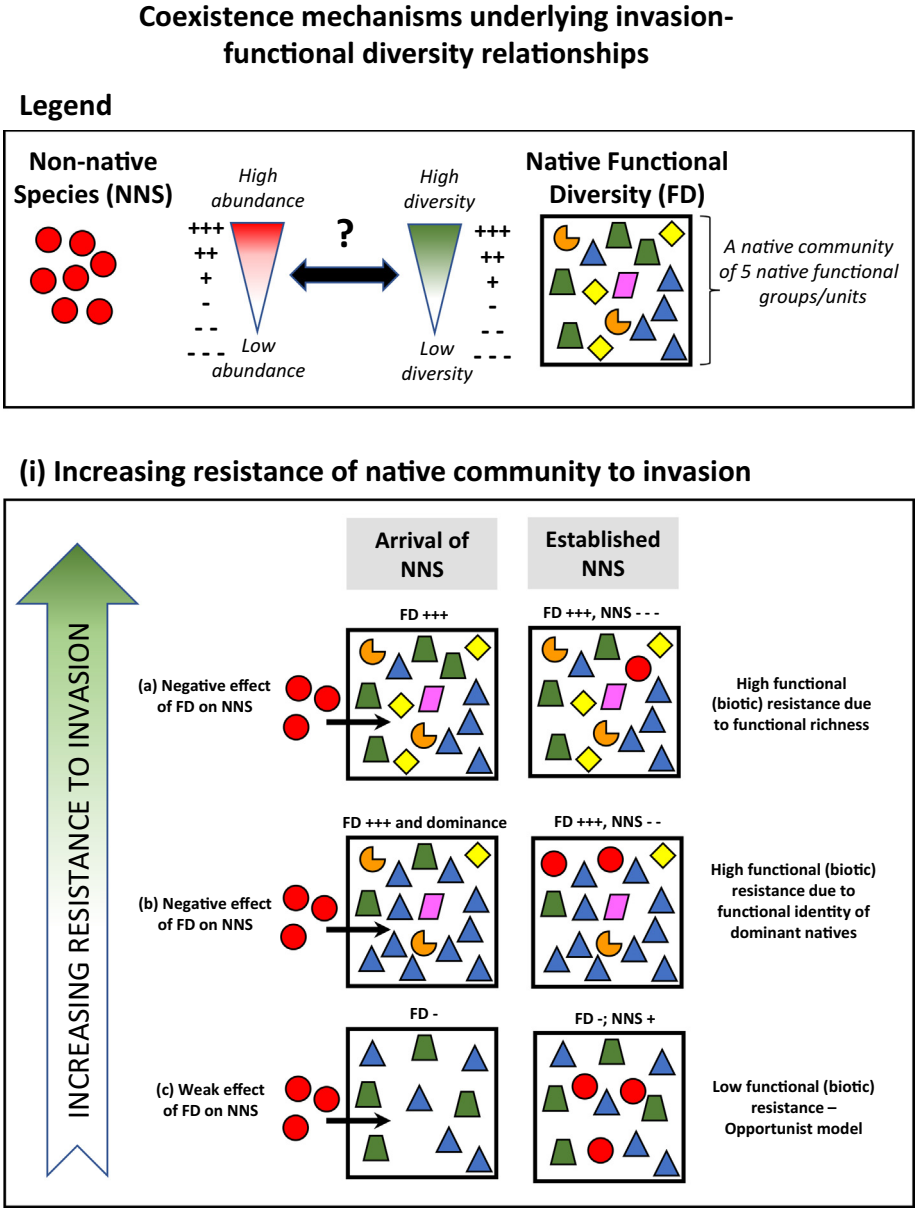


Fig. 2. Schematic representations of coexistence mechanisms underlying invasion-Functional Diversity relationships. The diagrams are ordered from (a) to (g) along a gradient of community resistance / invader impact.

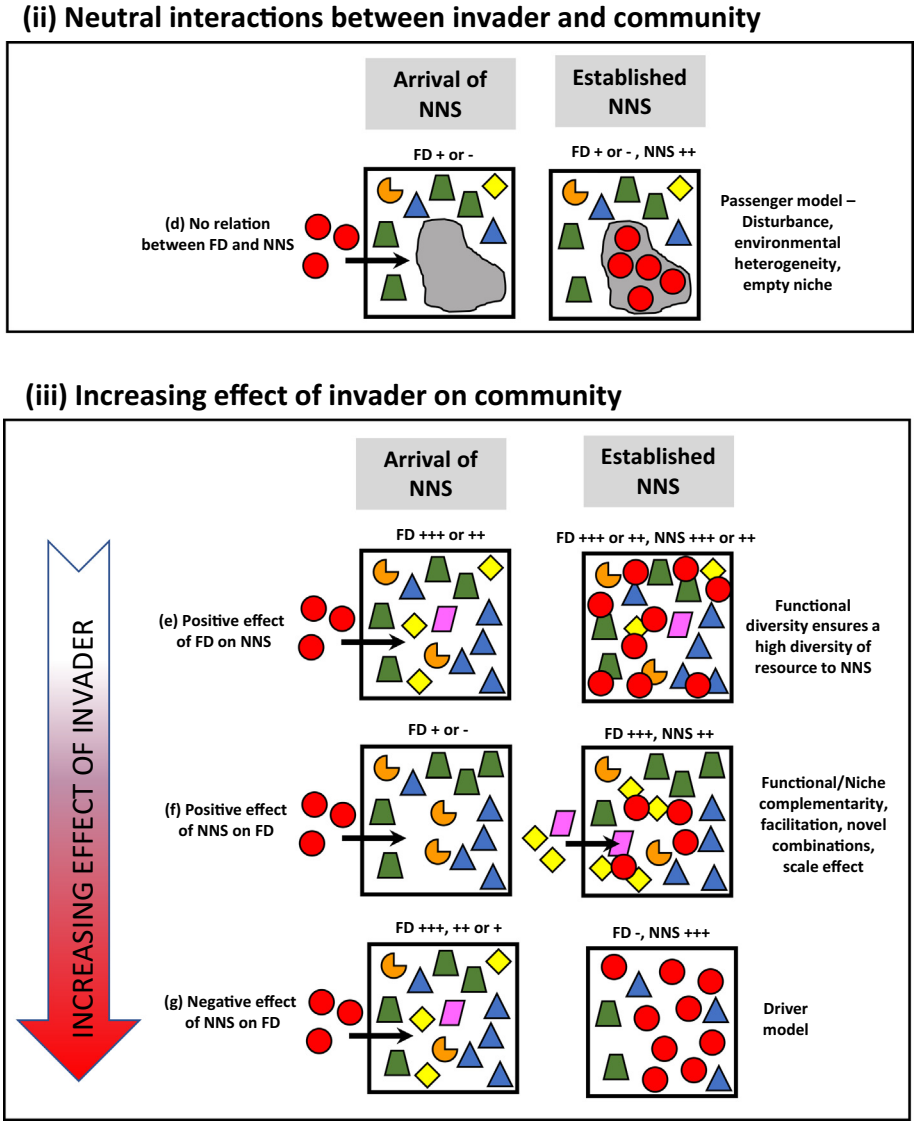


Fig. 2 (*continued*).

both timing and plasticity between native and invasive plants can also promote invasion success and persistence under climate change (Zettlemoyer et al., 2019). The invasive species may even occupy empty niches and increase FD (Williamson, 1996; Stachowicz and Tilman, 2005) when the functional originality of its traits is particularly high as compared with those of the organisms of the invaded community. This is exemplified by the invasion of Europe by the fruit fly *Drosophila suzukii*, which is able to use unripe and ripening fruits before the other native *Drosophila* spp. feeding on ripe and rotting fruits (Poyet et al., 2014). These empty niches, as referred to as 'opportunity windows', in ephemeral habitats (Johnstone, 1986) can also be observed in disturbed sites (Bonanomi et al., 2018 and see Section 3.3.4 below). Importantly, the trophic level of the invasive species may also drive the impacts they will have on species from recipient communities, with invasive species from equivalent or higher trophic levels than those of natives having stronger adverse effects (Bradley et al., 2019). For instance, the invasion of rivers by the crayfish *Pacifastacus leniusculus* significantly affects the structure of invaded communities and decreases invertebrate functional redundancy, with cascading consequences for leaf litter breakdown (Carvalho et al., 2022). The need for considering the trophic position of the invaders when assessing and predicting their impacts on functional diversity was formerly stressed by Chapin III et al. (1996). Here, whenever possible, we additionally re-emphasise the need for conducting ecosystem-based approaches to harness a consistent overview of the implications invasive species have for functional diversity, and the trophic cascades.

While functional dissimilarity should reduce native-invader competition, and increase the invasion rate (but see Kuczynski and Grenouillet, 2018, Pearson et al., 2018 who also reported that environmental filtering is significantly driving community assembly rules) a range of studies demonstrated that invaders induce functional trait convergence, possibly reducing FD, in the recipient community (see, for instance, the example of the common milkweed *Asclepias syriaca* affecting spider communities after introduction, Kapilkumar et al., 2019; or the Canadian goldenrod *Solidago canadensis* invading plant communities, Wang et al., 2019). The convergence of species traits can principally be explained by habitat filtering (Dyderski and Jagodziński, 2019). Alternatively, the invader can directly homogenize the composition of the community (Kapilkumar et al., 2019), in turn leading to functional convergence.

Literature on the use of FD indices in the context of biological invasions suggests that plant invasions are most often explained by the empty niche hypothesis (Fig. 2-d) rather than by the competitive hierarchy hypothesis (Fig. 2-a and g when the invader is respectively the loser and winner of this competition) (Loiola et al., 2018). However, both species-based and trait-based approaches revealed that the co-occurrence of native and invasive species could actually be the result of processes described by different hypotheses (Chabrerie et al., 2008; Chabrerie et al., 2010). Castro-Díez et al. (2016)

showed that *Carpobrotus* sp., which is woody and evergreen, reduces the frequency of tall, woody, N-fixing and evergreen native plants. This result agrees both with the habitat filtering hypothesis (here, tall N-fixing traits) and the niche differentiation hypothesis which states that competition is the main process determining establishment success, with species displaying different traits being able to coexist with the invader (here, different to woody evergreen traits). Thus, functional originality is expected to reduce the õimpacts of an invader on the community by reducing competition. However, in predator-prey systems, functional originality can harbour substantial impacts. An example concerns invasive predators on islands that lack trophic analogues, conferring high impact due to prey naivete (Anton et al., 2020). For invasive prey, predator naivete could promote invasion success if prey are avoided by natural enemies (Cuthbert et al., 2018). Finally, by looking at the traits of persisting and declining plants in invaded communities, Fried et al. (2019) found that niche differentiation and competitive hierarchy (in terms of height and regeneration strategy of the plants) are important factors causing persistence or decline of the native plants.

3.3.3. Using functional diversity indices to better describe novel species combinations and changes in mutualistic interactions?

While invasive species presumably affect biodiversity at different spatio-temporal scales, it is not necessarily true that they also decrease community functions by inducing native species loss or extinction (Stohlgren et al., 2008; Thomas and Palmer, 2015). Indeed, the number and abundance of invaders can even be positively correlated to FD (Wang et al., 2018), and adding new species and traits to local species assemblages can mechanically increase FD, both at local and regional scales. At the local scale, the FD of plant communities can be increased under greater invasion conditions, leading to a more efficient use of resources at the interspecific level via niche complementarity (Flinn et al., 2017; Wang et al., 2018).

Novel species combinations and mutualism can directly or indirectly increase the FD of other ecosystem components (e.g. the invader provides a new resource to the system) (Fig. 2-f). For example, Lekberg et al. (2013) showed that invasions by the spotted knapweed *Centaurea stoebe* and by the leafy spurge *Euphorbia esula* induced a higher abundance and diversity of symbiotic arbuscular mycorrhizal fungi. In this way, invasive species enrich ecosystems with new species and new functions, contributing to increase FD. Importantly, novel combinations between invasive and native organisms might increase ecosystem diversity. For instance, invasive trees may form novel associations with fungal associates of native flora (Tedersoo et al., 2007; Bahram et al., 2013), or re-establish symbioses with cosmopolitan species (Dickie et al., 2010). By changing the soil through root exudates (Kulmatiski et al., 2008), favouring nutrient uptake (Castro-Díez et al., 2016) or by attracting pollinators (Stouffer et al., 2014) and frugivorous species (Poyet et al., 2014), invasive plant species can directly favour the establishment of new species. However, these facilitations among species could also result in an invasional meltdown (e.g., Crane et al., 2020). Contrastingly, the inhibition of native mutualists, “mutualism disruption hypothesis”, can also promote invaders with a competitive advantage over mutualism-dependent native species. Indeed, introduced plants are often transported with a greatly reduced number of associated organisms, including many symbiotic mutualists (Dickie et al., 2017). For example Dickie et al. (2017) found a lower FD, and more variable composition of fungal associates, with non-native trees in New-Zealand. The reduction of diversity of symbionts may limit plant nutrient uptake and subsequently affect biodiversity. In some cases, this lack of FD seems to have little consequence (Hayward et al., 2015): *Pinus* associating with a highly simplified fungal community may not be limited by a loss of symbiont diversity (Hayward et al., 2015). Overall, the available literature suggests that interactions between invasive and native taxa could have cascading effects across trophic levels (Thomsen et al., 2014) and can lead to evolutionary changes (Rodriguez, 2006). Novel insights into these effects are likely to be obtained by the increasing use of FD indices in biological invasion studies.

3.3.4. Linking the effects of invasion to ecosystem properties

FD indices can be conveniently used for linking the effects of an invader on ecosystem functioning. Positive or negative correlation of FD indices with abiotic parameters, such as soil organic carbon, total nitrogen, moisture, etc. may highlight the role of invaders on ecosystem property changes (Castro-Díez et al., 2016). For example, a negative correlation between FRic and soil organic C pinpoints the slower mineralization of organic matter in the presence of the invader (*Carpobrotus* sp.; Castro-Díez et al., 2016). A negative correlation of functional redundancy with soil nitrogen and moisture suggests a higher depletion of soil resources when *Carpobrotus* sp. and native species share the same combination of trait values (Castro-Díez et al., 2016). Luan et al. (2021) recently reported that the invasive woody grass, Moso bamboo *Phyllostachys edulis*, changes the functional diversity of decomposers (estimated with functional groups by controlling the mesh size of litterbags) and consequently alters litter decomposition in forest sites across a wide climate gradient. Although much evidence is provided by soil ecology studies, examples of cascading impacts of invasive species on functional diversity, and then ecosystem properties, are also frequent in freshwater habitats. For instance, Carvalho et al. (2022) showed that higher crayfish abundance (*Pacifastacus leniusculus*) led to a decrease in invertebrate functional redundancy and disrupted detritus-based food webs by affecting leaf breakdown. However, given the range of abiotic parameters that could be altered by invasion, further work must be undertaken to improve understandings of how species traits and environmental variables interact. Reciprocally, the effects of abiotic parameters on FD indices should be quantified in an invasion context.

3.4. Combining effects of environmental conditions and biological invasions on functional diversity

As described in the above sections, FD indices reveal the reciprocal relationship between an organism and its environment, and thus can be conveniently used for assessing the effects of environmental filtering, including the effects of global change on the FD of organisms. For instance, Cantarel et al. (2013) simulated changes in climatic conditions over four years, and demonstrated that warming had no effect on plant species diversity, but affected plant traits and FD, with potential consequences on plant-plant interactions. In another plant study, Laliberté et al. (2010) focused on the intensification of land-use, and concluded that functional redundancy was greatly affected by such environmental disturbance. Using functional originality and uniqueness, Buisson et al. (2013) found that fish species with the most unique traits are not necessarily those that would be threatened by climate change, while individual species range shifts lead simultaneously to both a severe decline in the functional diversity and an increase in the functional similarity within and among fish communities. In general, similar changes in FD patterns are reported across a wide range of taxa: a reduction of FD has been reported in reef fish communities (Martins et al., 2012), zooplankton (Barnett and Beisner, 2007), macrophytes (Fu et al., 2014), invertebrates (Schriever et al., 2015) and fishes (Mason et al., 2007) when dealing with ecological filtering. While FD indices are being increasingly used in the context of biological invasions, the combined impacts of environmental change and biological invasions on FD is still lacking examination (Colin et al., 2018).

Environmental disturbances and biotic interactions are key drivers of spatial heterogeneity within communities (Kumar et al., 2006). The heterogeneity caused by disturbances is likely to increase invasion risks due to increased stochasticity that prompts regime shifts in communities. Nevertheless, it could also limit the ecological impact of invasive species, by promoting coexistence mechanisms between native and invasive species that cannot occur in more homogeneous environments (Snyder and Chesson, 2003; Melbourne et al., 2007; Ricciardi et al., 2013). In the rare studies that have considered the joint effects of environmental factors and invasive species on FD of the colonized community, FRic and FDiv are often reported as having the greater discriminatory power, with FD values being generally lower than expected in disturbed habitats (Mason and de Bello, 2013). Seasonal variations were found to decrease FRic of flowering plants, especially in invaded plant

communities (Fried et al., 2019). Not surprisingly, temperature has a strong effect on the FD of communities composed of ectothermic and plant species, and thermal conditions have been found to drive the effects of non-native species in the recipient community. Specifically, by calculating CWM from four functional traits, Helsen et al. (2018) reported that warmer environmental conditions positively affected litter decomposition of invasive plants, and this process was associated with lower plant available nitrogen. Conversely, a reduced litter decomposition was measured in colder regions, possibly resulting from the lower litter quality and the allelopathic effects of the non-native plant (Helsen et al., 2018).

Multiple habitat disturbances favour the establishment of non-native species, in line with the definition of invasive species being mediated by man-made environmental changes (Didham et al., 2005, MacDougall and Turkington, 2005; Fig. 2d). A positive relationship between habitat disturbance, non-native species, TD and FD has been observed by Escobedo et al. (2017). Conversely, native species FD decreased with habitat disturbance in another study (Murphy et al., 2006). Disturbances may additionally contribute to removing native plant and tree species that can be replaced by annual and perennial non-native species, as reported by Bonanomi et al. (2018), who examined the effects of a stand-replacing windstorm that affected a holm oak *Quercus ilex* community; here, the recolonization of empty niches by non-native trees drove new successional ecological trajectories that reshaped community identity and the associated FD. The results from Mandle and Ticktin (2015) supported the idea of an increase of the overall FD in disturbed habitats in the presence of non-native species. In those disturbed habitats, a higher functional redundancy among species (native and non-natives) subsequently increases the community resilience (Pillar et al., 2013) and ecological stability (Biggs et al. 2020). Functional evenness and functional divergence indices can be computed for decrypting early effects of perturbation on communities (Mouillot et al., 2013). In ecosystems with high levels of human disturbance, empty windows created in the functional space of the community may provide opportunities for non-native species to integrate functionally altered species assemblages. To detect this phenomenon and the use of the functional gap in recipient communities by the invader, we also recommend using multivariate trait analyses of invaded communities (Toussaint et al., 2018), to represent the average position of the invader in the functional space and examine its coincidence with a potential community functional gap.

When habitats are disturbed, functional traits of native organisms are first shaped by the local environmental gradients (for instance soil acidity, Chabrerie et al., 2010), and then by the invader dominance, if invaded. As disturbance often acts as a significant environmental filter, co-occurring species, either native or non-native, are expected to exhibit a large overlap in their performing traits. Consistently, Escobedo et al. (2017) found that soil disturbance by rodent burrowing increases trait convergence in both native and non-native plants. Another example has been reported by Mandle and Ticktin (2015) who found a higher prevalence of plant species with physical defences as a consequence of habitat disturbance (in their study: livestock-grazed habitats), with non-native species further contributing to the reduction of clonality. At the local scale, disturbances generally interact in a complex way with environmental conditions and spatial community heterogeneity to create a patchwork of recruitment opportunities for invasive species (Mazía et al., 2019). At the landscape (Chabrerie et al., 2007) and regional (Deutschewitz et al., 2003) scales, disturbances and functional heterogeneity of habitat mosaic are major predictors of invasion patterns.

In the context of biological invasions, there are no studies that tried to tease apart the effects of non-native species on the FD of an invaded community from other interacting environmental disturbances. In these ecological situations, we expect that the impacts on FD would greatly vary, and would highly depend on (i) the strength and nature of habitat disturbance and environmental filters than can select for specific functional attributes, (ii) the functional identity of the community, (iii) the characteristics of the invader(s), and (iv) the invasion stage. As a result, it is very likely that the main conclusions of studies would be case-specific. To deal with multiple environmental factors, mathematical approaches have been used to determine those most probably driving the observed changes in FD (Mason and Mouillot, 2013). For instance, Colin et al. (2018) used hierarchical partitioning models and generalized linear mixed models to rank the relative contribution of multiple environmental parameters on FD indices of fish assemblages. They found that altitude, habitat degradation and non-native fish biomass were ordered differently, and reported that altitude and biomass of non-native fish influenced both FSpe and FOri, while habitat degradation shaped FSpe only.

3.5. Evaluating the effects of invasive species removal

The removal of invaders increases native and overall TD compared with invaded areas, especially if the invader was dominant because it can reduce suppressive effects on resident species, reduce allelopathy or competition for resources, or because invaders can alter the habitat, movements or resources (see the examples of the removal of *Cirsium arvense*, *Humulus japonicus*, *Lonicera maackii*, *Melilotus* spp., *Pittosporum undulatum*; Barber et al., 2017, McNeish et al., 2017, O'Leary et al., 2018, Fried et al., 2019; Fig. 3a,b). After a rapid increase, TD usually decreases until reaching a new ecological equilibrium, towards a state similar to that of reference communities (Barber et al., 2017; O'Leary et al., 2018; Fried et al., 2019; Fig. 3c). Functional richness is correlated to TD, and often presents similar variations over time (Barber et al., 2017). A declining taxonomic richness is somewhat expected to be correlated with a declining functional richness, since a limited number of species would be expected to have a more restricted number of trait values. The high initial functional richness following invader removal may be due to rare species that failed to establish in the long-term (Gerisch et al., 2012; Barber et al., 2017). In some cases, invasive species removal can lead to dissimilar taxonomic and functional diversity patterns (McNeish et al., 2017, Fried et al., 2019; Fig. 3d). McNeish et al. (2017) showed that removing the plant invader *Lonicera maackii* resulted in a higher macro-invertebrate TD, while it decreased macro-invertebrate community FRic in autumn and winter, in restored streams as compared with invaded ones. This result is explained by the availability of resources, with increased light conditions on the stream after removal of the invader resulting in a shift from heterotrophic microbes to periphyton communities, in turn affecting food web dynamics. Functional divergence is expected to increase after the removal of an invasive species, as native species recolonize the restored sites; higher functional divergence suggests niche differentiation in established communities (Barber et al., 2017).

When invader removal is associated with additional restoration measures, such as native seed sowing, FD is subsequently highly influenced by the characteristics of the selected species, if they manage to establish. Tölgyesi et al. (2019) showed that when restoration treatments were conducted by seed sowing of three native grasses, or perennial-crop–mediated restoration, TD and functional richness often remained lower than in their reference sites. Further, spontaneous recovery showed little difference with the reference sites, in particular for FD and CWM, as sown species limit the establishment of other taxa. Even if sowing did not hamper the recovery of some aspects of FD, e.g. functional divergence or evenness, species and functional richness can remain lower for decades as compared with other restoration methods (Tölgyesi et al., 2019). These investigations illustrate the added value of computing trait-based indices for the evaluation of restoration success, and provide useful guidelines for practitioners.

Restoration aims at helping the recovery of the communities towards the reference (non-invaded) ones. Rehabilitation, however, aims at reinstating a level of ecosystem functionality (McDonald et al., 2016). Mandle and Ticktin (2015) warned us about adopting FD as a management target. The specific aspect of FD that will be restored is also a critical consideration in the context of ecosystem functionality. Non-native species can possess novel combinations of functional traits that will increase FD at first, but may become dominant with negative consequences for ecosystem functioning and resilience in the long-term. Furthermore, these actions could promote non-target spread of non-native species, which could further affect native biodiversity and FD elsewhere.

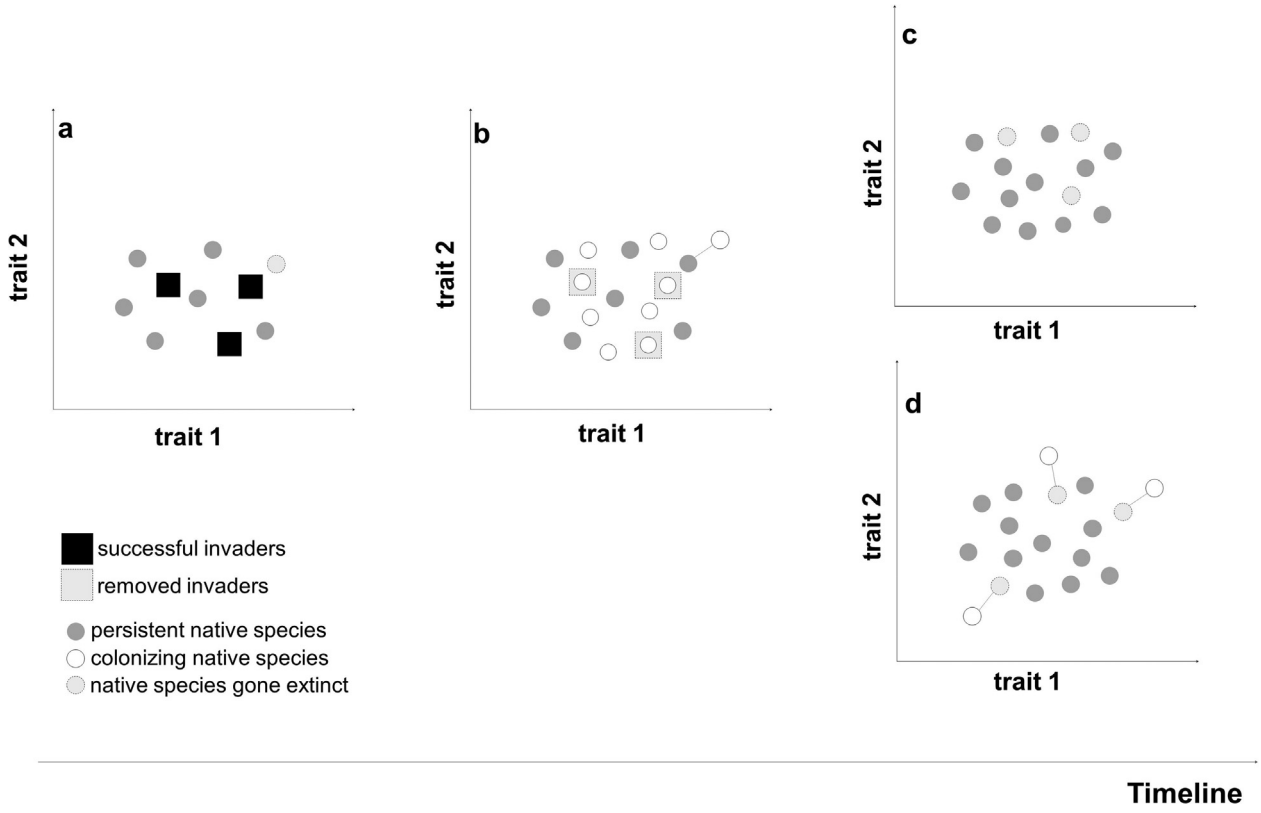


Fig. 3. Schematic representations of functional trait distributions and their change in response to invasive species removal over time. Species are represented in a 2D trait space with circles as natives and squares as invaders. Persistent native species are filled in grey, while new colonizing native species are filled in white. Successful invaders are black-filled squares, and natives and invaders that have gone extinct are represented using dotted circles or squares, respectively.
The following cases are represented: (a) before invader removal, (b) in the short term after invader removal, where taxonomic and functional diversity increases (natives recolonizing their niche and newly arrived natives filling vacant niches), and in the long term after invader removal (c and d), where (c) native taxonomic and functional diversity decrease (mainly due to rare species failing to establish), and (d) native functional divergence and dissimilarity increase. The case of secondary invasion is not depicted.

4. Perspectives

Despite increasing evidence of FD being a powerful and useful tool for both testing ecological hypotheses on biological invasions (e.g. coexistence theory, Fried et al., 2019) and predicting future scenarios of invasion (i.e. identify which species are more likely to become invasive in the future, Gallien and Carboni, 2017), so far its potential has only been partly explored (Pavoine and Bonsall, 2011; Gallien and Carboni, 2017). Here, we therefore suggest novel directions to advance FD, which we hope will further stimulate the use of FD indices in the context of biological invasions (Fig. 4).

4.1. From functional diversity to interaction diversity? A network perspective

Taking functional and phylogenetic diversities into account, rather than only focusing on taxonomic diversity, is a substantial improvement over classic methods of ecological assessment. It has proved useful in a variety of contexts, from the mapping of evolutionary potential (Forest et al., 2007) to the understanding of invasive species impacts on native communities (Toussaint et al., 2018). The next step, however, is to also incorporate data on ecological networks and interaction diversity, especially in the context of biological invasions (Pantel et al., 2017; Smith-Ramesh et al., 2017), and with a view towards the monitoring of ecosystem services (Bohan et al., 2016). Indeed, invasions can have very different effects on food webs and their component species, from causing the extinction of native prey or competitors, to initiating an invasion meltdown at multiple trophic levels or differentially affecting species across the food chain (David et al., 2017). For instance, Thomsen et al. (2014) conducted a meta-analysis of 56 field experiments that examined the effects of marine invaders on local diversity and showed that invaders typically have negative effects on biodiversity within a trophic level, but positive effects on biodiversity of higher trophic levels. They additionally suggest that positive effects on higher trophic levels could be driven by habitat-formation and food provision.

Theoretical models suggest that invasion success and robustness against the detrimental effects of invasions can be partly predicted by network properties and the position of species in community networks (Romanuk et al., 2009; Romanuk et al., 2017). While some studies have evinced species trait relationships and links among species (e.g. Gravel et al., 2013), functional diversity indices are not necessarily good predictors of network properties, nor of functions supported by the network (e.g. pollination, Garibaldi et al., 2015). Moreover, the necessity of measured traits to be common among considered species can limit the assessment of interactions between different trophic levels or functional groups of species (e.g. plants and pollinators) through functional traits only. Thus, a true grasp of the functioning and complexity of ecosystems, and of species invasion impacts in particular, calls for the assessment of interaction diversity (ID) together with other diversities. To that end, recent modelling developments now allow the computation of multiple indices of interaction diversity (Legras et al., 2019). The initial proposal of Novotny (2009) and Poisot et al. (2012) aimed at counting the number of nodes and links shared between networks, and this has been developed by Trøjelsgaard et al. (2015) and Pellissier et al. (2018), and advanced further by Ohlmann et al. (2019). This framework is centred on the notion of the beta-diversity of interaction networks, but also allows the full partition of interaction diversity into alpha and gamma components at different scales (individual or aggregated networks, using species or groups of species as nodes, Ohlmann et al., 2019). In the context of species invasions, such a framework might help in understanding how ecological networks are rewired by the arrival of

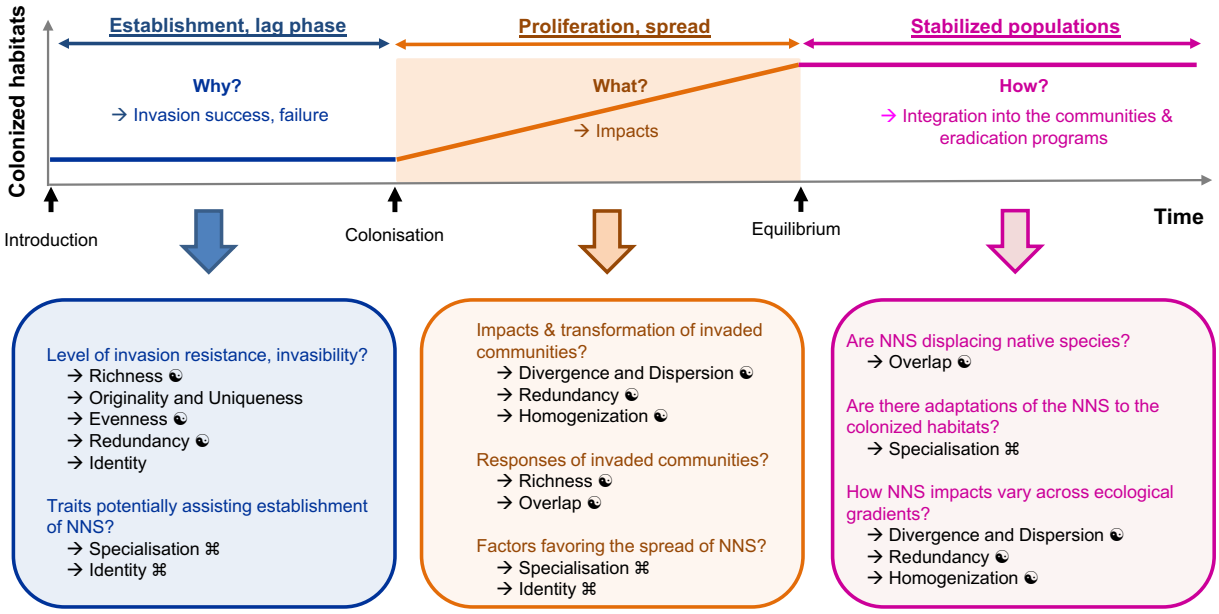


Fig. 4. Along the invasion continuum, the use of functional diversity indices can greatly contribute to improve our understanding of the basics tenets of biological invasions. At the initial stages, investigations often examine the main factors favouring introduction and establishment (Why are some communities / habitats more susceptible to invasion? Why are some non-native species more successful?). During proliferation and spread, the questions often focus on transformations of invaded communities / foodwebs / ecosystems (What are the effects, impacts?). Finally, when non-native species have colonized several communities / localities and have stabilized populations, studies examine the place taken by non-native species (How much are non-native species integrated into different ecological networks / facilitate establishment of other non-native species), and try to predict the novel ecological equilibrium that could be reached if mitigation measures are taken (How much ecological restoration would contribute to reverse the perturbation?). For each question/topic, a range of best suited functional metrics to be used is proposed. See Table 1 for the definition of each indicator and some of the expectations regarding the results they may provide.
☯ FD indices computed at the community level
⌘ FD indices computed at the species level
Additional questions, alongside with the functional indicators that can be used, include: (1) What are the range of values and amount of space (volume) of the measured trait (s)? Richness; (2) Are there differences among non-native and native species traits? Divergence, Dissimilarity, Dispersion, Overlap, Dissimilarity; (3) Can traits explain invasion success and impacts? Evenness, Dissimilarity, Specialisation.
The assessment of functional indicators (indices) can be illustrated with three main representation types: the distribution of trait attributes, the functional space or hypervolume (binary or probabilistic), the functional tree or dendrogram. For hypervolumes, PCA/PCoA or convex hull can be used. Dendrogram and NMDS can be used to represent distances among species or communities. Importantly, the choice of the representation will be driven by the nature of the index, and in some instances, there is no need for an illustration because the interpretation of the indices is based on a statistical/null model.

non-native species (see e.g. the type of data obtained by Strong and Leroux, 2014).

Another methodological framework that can help identify the functional role of species within networks – and that could be readily applied to invasive species – is that of motif analyses, initially developed in physics (Kashtan et al., 2004), but adapted to the study of food webs (Stouffer et al., 2007) and bipartite networks (Simmons et al., 2019; Ouadah et al., 2022). In this framework, each motif (i.e. arrangement of links among a given set of nodes) of a given size (e.g. all motifs involving exactly three nodes in food webs, Stouffer et al., 2007) is counted and normalized by the combinatorial maximum (or by expectations obtained from node degree distribution, Ouadah et al., 2022). The profile of these motif counts can inform about regularities observed in different networks. Moreover, each unique position within these motifs can be identified and the vector of counts of every position for each species then yields a representation of a species' role, which can be used to address questions related to shifts of species functions within ecosystems (Stouffer et al., 2012).

4.2. Driven by data: opportunities and constraints in the context of biological invasions

Considering the requirements of functional diversity indices, the availability of sufficient data can be a crucial issue hindering the application of diversity-based approaches to invasion biology. Indeed, since invaded ecosystems are often fragile, and negatively affected, sampling native communities might be difficult (i.e. if sampling is lethal), at least to obtain sufficient replicates of trait measurements needed for the computation of FD indices. In the initial stages of invasion, low density invasive species might also elude sampling (McCarthy et al., 2013), thus prohibiting the use of indices based on intraspecific trait variability and/or estimates of species abundances. The identification of non-native species can also introduce problems, especially when these non-natives are part of cryptic species complexes and/or display very high phenotypic variability. Nevertheless, the present paucity of FD studies for many ecosystem types and taxonomic groups calls for a greater research effort across a range of contexts. Indeed, given that studies hitherto have often produced equivocal, context-dependent results, further work is urgently required to deduce potential generalities in FD measures within the context of invasions, to aid predictive efforts. Such investigations should also seek to use standardized, robust methods to make results comparable across systems.

As mentioned in Section 2, the paucity of trait data can bias FD estimation. This is particularly true for biological invasions, for which the use of trait databases (Plants: TRY, Kattge et al., 2020, soil invertebrates: BETSI, Pey et al., 2014) might help compare local community diversity to "references" external to the study location (and thus evince potential changes due to existing invaders). Conversely, using external data is not without pitfalls because of e.g. intraspecific variation. For instance, using trait values from a different location than that of the studied communities to compensate for the paucity of data could bias the estimation of functional diversity. This is particularly the case for biological invasions, where functional attributes of invaders might change from those in their native range or native species might respond to invasions with niche displacement. Overall,

generating intraspecific trait variability from global databases can be problematic, thus preventing the use of FD indices based on intraspecific variability (such as functional range measures of functional richness). Misattributions of species traits, geographical inaccuracies and/or misidentification of species identity can also lead to spurious results that are more difficult to detect when data come from global databases (as e.g. in the case of species distributions from global databases, Maldonado et al., 2015).

Finally, global databases grow all the more rapidly as they are filled with data on readily-measurable traits (e.g. plant traits that could be measured from space, Jetz et al., 2016). Conversely, traits that prove difficult to be measured in the field might also be very difficult to obtain from such global databases. Next-generation sequencing (NGS) technologies might help invasion biology circumvent its current problems, aiding identifications and improving sample sizes. Indeed, NGS now offers a palette of solutions which can greatly ease mass biomonitoring (Derocles et al., 2018). In particular, such techniques will prove useful to move from functional to interaction diversity approaches, as suggested above, because NGS techniques can be easily combined with automated network-building algorithms (Vacher et al., 2016; Pauvert et al., 2019; Makiola et al., 2020; Dubart et al., 2021).

4.3. Towards predictive or explanatory models of invader impacts?

Diversity-based approaches to community dynamics are but one framework available to understand and predict the impacts of non-native species on ecosystems (Gallien and Carboni, 2017). Owing to diversity-based approaches which can be computed to assess the effect of invasions on the different facets of species diversity (Romanuk et al., 2017) (Fig. 4), it is possible to produce both *explanatory* (with a view to the understanding of ecological mechanisms) and *predictive* (aiming at the extrapolation of future patterns) models of invader impacts on ecosystems.

While explanatory models dominate the literature in community ecology – and more predictive models have thus been urged (Mouquet et al., 2015) – invasion biology conversely strives primarily towards predictive models (Kareiva, 1996; Leung et al., 2004; Hattab et al., 2017). For instance, new machine learning models using multivariate data on invasive species have been applied to predict what species will become invasive and where, based on traits and phylogenies (Fournier et al., 2019). In a world of global changes, with climate change effects interacting with increasingly frequent species invasions (Alexander et al., 2015; Pauchard et al., 2016), ecologists must be proactive rather than reactive (Bellard et al., 2016). While the current focus of such studies lies with "where" invasion will occur and how best to prevent it, future research should also be concerned with the prediction of effects on ecosystems, i.e. functional aspects linked to invasions. In the existing FD framework, some studies have begun addressing similar effects (Leitão et al., 2016), and have shown that rare species contribute disproportionately to functional diversity, thus hinting at the fragility of ecosystems in the face of future disturbances. However, their methods primarily rely on virtual species removal and the computation of changes in FD indices. This is acceptable as a first step, in the same way that virtual species removal in ecological networks has long been used to gauge the potential for cascading extinctions in e.g. food webs or plant-pollinator networks (Pocock et al., 2012; Astegiano et al., 2015). However, accounting for post-invasion niche displacement – similarly to accounting for network rewiring post-disturbance – should now lead to new methodological developments aimed at predicting how species' functional traits will change after invasion.

Despite debates around invasion biology as a science (Davis et al., 2011; Valéry et al., 2013; Simberloff and Vitule, 2014; Cuthbert et al., 2020), studies on invasive species have continued uncovering the processes behind species invasiveness and ecosystem invasibility, with wider relevance for community ecology (Alpert et al., 2000; Milbau and Nijs, 2004; Richardson and Pyšek, 2006; Catford et al., 2019). Meanwhile, as evinced by our review of the literature, invasion biology has started to grapple with the concepts of functional and phylogenetic diversities. A logical roadmap for studies on the impacts of non-native species now points towards further integration of diversity-based approaches into invasiveness/invasibility studies, with a view towards an understanding of how ecological networks (and the functions of species within them) can explain resistance to invasion and the impacts of invaders (Pantel et al., 2017). Equipped with these advances from FD-based explanatory models of species invasions, predictive models will undoubtedly gain in their ability to extrapolate future conditions, and thus become more useful in this era of global changes.

5. Conclusions

(1) Our review has synthesized the literature aiming at describing the effects of biological invasions on the functional diversity of recipient communities. Overall, while advancing rapidly, we propose increased study effort into the use of FD to test invasion hypotheses, as well as to better understand invasion success and impacts under relevant contexts, with a view to predict future scenarios. In particular, future studies should seek to incorporate data on ecological networks and interaction diversity in the context of invasions and employ advances, such as Next-Generation Sequencing (NGS), in discerning traits.
(2) We found that functional diversity may strongly vary at the onset of the invader community colonization, while it stabilizes at intermediate and high levels of invasion. In future studies, having additional information on the invasion stage (early invasion, lag phase, naturalization) would provide further insights, as this greatly influences functional diversity metrics (Fig. 4).
(3) Studies exploring the functional difference between organisms from the recipient communities and invaders of the same trophic levels are still uncommon, although it has been observed that functional differences can favour certain invasive species over native ones in a climate change context. In parallel, future studies should compare the nature of the effects of non-native organism establishment into a novel or non-analogue community to establishment in an analogue community.
(4) The functional changes that occur in invaded communities during the lag phase of an invasion have been poorly investigated, and it remains to be determined if there are consistent changes in FD metrics that could indicate the end of the lag phase; or, conversely, unchanged indices that could be associated with the maintenance of the lag phase.
(5) In sum, we recommend that future studies consider computing functional diversity indices, as they represent valuable tools for obtaining in-depth diagnostics of community structure and functioning, as well as the implementation of efficient restoration plans and conservation strategies.

CRediT authorship contribution statement

DR, FM, MM: Conceptualization; DR: Funding acquisition and Project administration; Visualization; All co-authors designed the figures / tables, wrote the original draft, reviewed and edited the text.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

The authors were supported by InEE-CNRS via a funded network dedicated to Biological Invasions (GdR CNRS 3647 Invasions Biologiques). DR, FM, and AKB are funded by the ASICS project (ANR-20-EBI5-0004, BiodivERsA, BiodivClim call 2019-2020). Insightful exchanges within the framework of the Programme IPEV 136 'Subanteco' (supported by the French Polar Institute Paul-Emile Victor, IPEV) have also stimulated the writing of this review. RNC acknowledges funding from the Alexander von Humboldt Foundation Postdoctoral Fellowship and Leverhulme Trust Early Career Fellowship (ECF-2021-001).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155102.

References

Ackerly, D., Knight, C., Weiss, S., Barton, K., Starmer, K., 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130, 449–457.

Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species' responses to climate change. Nature 525, 515.

Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. System. 3, 52–66.

Anton, A., Geraldi, N.R., Ricciardi, A., Dick, J.T.A., 2020. Global determinants of prey naiveté to exotic predators. Proc. R. Soc. B Biol. Sci. 287, 20192978.

Arenas, F., Sánchez, I., Hawkins, S.J., Jenkins, S.R., 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87, 2851–2861.

Astegiano, J., Massol, F., Vidal, M.M., Cheptou, P.-O., Guimarães Jr., P.R., 2015. The robustness of plant-pollinator assemblages: linking plant interaction patterns and sensitivity to pollinator loss. PLoS One 10, e0117243.

Bahram, M., Kõljalg, U., Kohout, P., Mirshahvaladi, S., Tedersoo, L., 2013. Ectomycorrhizal fungi of exotic pine plantations in relation to native host trees in Iran: evidence of host range expansion by local symbionts to distantly related host taxa. Mycorrhiza 23, 11–19.

Barber, N.A., Lamagdeleine-Dent, K.A., Willand, J.E., Jones, H.P., McCravy, K.W., 2017. Species and functional trait re-assembly of ground beetle communities in restored grasslands. Biodiversity and Conservation 26, 3481–3498.

Barnett, A., Beisner, B.E., 2007. Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. Ecology 88, 1675–1686.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Henriques-Silva, R., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C., Crujeiras, R., 2022. betapart: partitioning beta diversity into turnover and nestedness components. R package ver. 1.5.6. <https://cran.r-project.org/web/packages/betapart/index.html>.

Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12.

Biggs, C.R., Yeager, L.A., Bolser, D.G., Bonsell, C., Dichiera, A.M., Hou, Z., Keyser, S.R., Khursigara, A.J., Lu, K., Muth, A.F., Negrete, B., Erisman, B.E., 2020. Does functional redundancy affect ecological stability and resilience? a review and meta-analysis. Ecosphere 11 (7), e03184. https://doi.org/10.1002/ecs2.3184.

de Bello, F., Lepš, J., Lavorel, S., Moretti, M., 2007. Importance of species abundance for assessment of trait composition: an example based on pollinator communities. Commun. Ecol. 8, 163–170.

de Bello, F., Lavergne, S., Meynard, C.N., Leps, J., Thuiller, W., 2010. The partitioning of diversity: showing Theseus a way out of the labyrinth. J. Veg. Sci. 21, 992–1000.

de Bello, F., Carmona, C.P., Dias, A.T., Götzenberger, L., Moretti, M., Berg, M.P., 2021. Handbook of Trait-based Ecology: From Theory to R Tools. Cambridge University Press.

Bjerknes, A.-L., Totland, Ø., Hegland, S.J., Nielsen, A., 2007. Do alien plant invasions really affect pollination success in native plant species? Biol. Conserv. 138, 1–12.

Blackburn, T.M., Bellard, C., Ricciardi, A., 2019. Alien versus native species as drivers of recent extinctions. Front. Ecol. Environ. 17, 203–207.

Blonder, B., 2018. Hypervolume concepts in niche- and trait-based ecology. Ecography 41, 1441–1455.

Blonder, B., Lamanna, C., Violle, C., Enquist, B.J., 2014. The n-dimensional hypervolume. Glob. Ecol. Biogeogr. 23, 595–609.

Bohan, D.A., Landuyt, D., Ma, A., Macfadyen, S., Martinet, V., Massol, F., McInerny, G., Montoya, J.M., Mulder, C., Pascual, U., Pocock, M.J.O., White, P., Blanchemanche, S., Bonkowski, M., Bretagnolle, V., Brönmark, C., Dicks, L., Dumbrell, A., Eisenhauer, N., Friberg, N., Gessner, M.O., Gill, R.J., Gray, C., Haughton, A., Ibanez, S., Jensen, J., Jeppesen, E., Jokela, J., Lacroix, G., Lannou, C., Lavorel, S., Le Galliard, J.-F., Lescourret, F., Liu, S., Loeuille, N., McLaughlin, O., Muggleton, S., Peñuelas, J., Petanidou, T., Petit, S., Pomati, F., Raffaelli, D., Rasmussen, J., Raybould, A., Reboud, X., Richard, G., Scherber, C., Scheu, S., Sutherland, W.J., Tamaddoni-Nezhad, A., ter Braak, C., Termansen, M., Thompson, M.S.A., Tscharntke, T., Vacher, C., van der Geest, H., Voigt, W., Vonk, J.A., Zhou, X., Woodward, G., 2016. Networking our way to better ecosystem service provision. Trends Ecol. Evol. 31, 105–115.

Bonanomi, G., Incerti, G., Abd El-Gawad, A., Sarker, T., Stinca, A., Motti, R., Cesarano, G., Teobaldelli, M., Saulino, L., Cona, F., Chirico, G., Mazzoleni, S., Saracino, A., 2018. Windstorm disturbance triggers multiple species invasion in an urban Mediterranean forest. iForest Biogeosci. Forest. 11, 64–71.

Borgy, B., Violle, C., Choler, P., Garnier, E., Kattge, J., Loranger, J., Amiaud, B., Cellier, P., Debarros, G., Denelle, P., Diquelou, S., Gachet, S., Jolivet, C., Lavorel, S., Lemauviel-Lavenant, S., Mikolajczak, A., Munoz, F., Olivier, J., Viovy, N., 2017. Sensitivity of community-level trait–environment relationships to data representativeness: a test for functional biogeography. Glob. Ecol. Biogeogr. 26, 729–739.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16, 533–540.

Bradley, B.A., Laginhas, B.B., Whitlock, R., Allen, J.M., Bates, A.E., Bernatchez, G., Diez, J.M., Early, R., Lenoir, J., Vilà, M., Sorte, C.J.B., 2019. Disentangling the abundance-impact relationship for invasive species. Proc. Natl. Acad. Sci. 116, 9919–9924.

Buckley, H.L., Day, N.J., Case, B.S., Lear, G., Ellison, A.M., 2018. Multivariate methods for testing hypotheses of temporal community dynamics. BioRxiv:362822.

Buisson, L., Grenouillet, G., Villéger, S., Canal, J., Laffaille, P., 2013. Toward a loss of functional diversity in stream fish assemblages under climate change. Glob. Chang. Biol. 19, 387–400.

Byun, C., de Blois, S., Brisson, J., 2013. Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. J. Ecol. 101, 128–139.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087.

Cantarel, A.A.M., Bloor, J.M.G., Soussana, J.-F., 2013. Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. J. Veg. Sci. 24, 113–126.

Carboni, M., Münkemüller, T., Gallien, L., Lavergne, S., Acosta, A., Thuiller, W., 2013. Darwin's naturalization hypothesis: scale matters in coastal plant communities. Ecography 36, 560–568.

Cardoso, P., Mammola, S., Rigal, F., Carvalho, J., 2021. BAT: Biodiversity Assessment Tools. R package version 2.4. 2.

Carmona, C.P., de Bello, F., Mason, N.W.H., Lepš, J., 2016. Traits without borders: integrating functional diversity across scales. Trends Ecol. Evol. 31, 382–394.

Carmona, C.P., de Bello, F., Mason, N.W.H., Lepš, J., 2019. Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. Ecology 100 (12), e02876. https://doi.org/10.1002/ecy.2876.

Carvalho, F., Pascoal, C., Cássio, F., Teixeira, A., Sousa, R., 2022. Combined per-capita and abundance effects of an invasive species on native invertebrate diversity and a key ecosystem process. Freshw. Biol. 00, 1–14.

Castro-Díez, P., Pauchard, A., Traveset, A., Vilà, M., 2016. Linking the impacts of plant invasion on community functional structure and ecosystem properties. J. Veg. Sci. 27, 1233–1242.

Catford, J.A., Smith, A.L., Wragg, P.D., Clark, A.T., Kosmala, M., Cavender-Bares, J., Reich, P.B., Tilman, D., 2019. Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. Ecol. Lett. 22, 593–604.

CBD, 2016. Convention on Biological Diversity, Programme of Work on Invasive Alien Species. Accessed November 13, 2017. Available at https://www.cbd.int/invasive.

Chabrerie, O., Roulier, F., Hoeblich, H., Sebert-Cuvillier, E., Closset-Kopp, D., Leblanc, I., Jaminon, J., Decocq, G., 2007. Defining patch mosaic functional types to predict invasion patterns in a forest landscape. Ecol. Appl. 17, 464–481.

Chabrerie, O., Verheyen, K., Saguez, R., Decocq, G., 2008. Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (Prunus serotina Ehrh.) invasion in a European temperate forest. Divers. Distrib. 14, 204–212.

Chabrerie, O., Loinard, J., Perrin, S., Saguez, R., Decocq, G., 2010. Impact of Prunus serotina invasion on understory functional diversity in a European temperate forest. Biol. Invasions 12, 1891–1907.

Chao, A., Chiu, C.-H., 2016. Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. Methods Ecol. Evol. 7, 919–928.

Chao, A., Chiu, C.-H., Hsieh, T.C., 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93, 2037–2051.

Chapin III, F.S., Reynolds, H.L., D'Antonio, C., Eckhart, V., 1996. The functional role of species in terrestrial ecosystems. In: Walker, B., Steffen, W. (Eds.), Global Change in Terrestrial Ecosystems. Cambridge University Press, Cambridge, pp. 403–428.

Chapuis, E., Lamy, T., Pointier, J.-P., Juillet, N., Ségard, A., Jarne, P., David, P., 2017. Bioinvasion triggers rapid evolution of life histories in freshwater snails. Am. Nat. 190, 694–706.

Clark, G.F., Johnston, E.L., 2011. Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. Ecol. Lett. 14, 52–57.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228.

Colin, N., Villéger, S., Wilkes, M., de Sostoa, A., Maceda-Veiga, A., 2018. Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages. Sci. Total Environ. 625, 861–871.

Connolly, J., Sebastià, M.-T., Kirwan, L., Finn, J.A., Llurba, R., Suter, M., Collins, R.P., Porqueddu, C., Helgadóttir, Á., Baadshaug, O.H., Bélanger, G., Black, A., Brophy, C., Čop, J., Dalmannsdóttir, S., Delgado, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B.E., Ghesquiere, A., Golinski, P., Grieu, P., Gustavsson, A.-M., Höglind, M., Huguenin-Elie, O., Jørgensen, M., Kadziuliene, Z., Lunnan, T., Nykanen-Kurki, P., Ribas, A., Taube, F., Thumm, U., De Vliegher, A., Lüscher, A., 2018. Weed suppression greatly increased by plant diversity in intensively managed grasslands: a continental-scale experiment. J. Appl. Ecol. 55, 852–862.

Cornwell, W.K., Schwilk, D.W., Ackerly, D.D., 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87, 1465–1471.

Crane, K., Coughlan, N.E., Cuthbert, R.N., Dick, J.T.A., Kregting, L., Ricciardi, A., MacIsaac, H.J., Reid, N., 2020. Friends of mine: an invasive freshwater mussel facilitates growth of invasive macrophytes and mediates their competitive interactions. Freshw. Biol. 65, 1063–1072.

Crystal-Ornelas, R., Lockwood, J.L., 2020. The 'known unknowns' of invasive species impact measurement. Biol. Invasions 22, 1513–1525.

Cucherousset, J., Olden, J.D., 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36, 215–230.

Cuthbert, R.N., Dickey, J.W.E., McMorrow, C., Laverty, C., Dick, J.T.A., 2018. Resistance is futile: lack of predator switching and a preference for native prey predict the success of an invasive prey species. R. Soc. Open Sci. 5, 180339.

Cuthbert, R.N., Bacher, S., Blackburn, T.M., Briski, E., Diagne, C., Dick, J.T.A., Essl, F., Genovesi, P., Haubrock, P.J., Latombe, G., Lenzner, B., Meinard, Y., Pauchard, A., Pyšek, P., Ricciardi, A., Richardson, D.M., Russell, J.C., Simberloff, D., Courchamp, F., 2020. Invasion costs, impacts, and human agency: response to Sagoff 2020. Conserv. Biol. 34, 1579–1582.

Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu. Rev. Ecol. Evol. Syst. 34, 183–211.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection. J. Murray, London.
David, P., Thébault, E., Anneville, O., Duyck, P.F., Chapuis, E., Loeuille, N., 2017. Impacts of invasive species on food webs: a review of empirical data. Pages 1-60. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), Advances in Ecological Research vol. 56 - Networks of Invasion: A Synthesis of Concepts. Academic Press.
Davies, K.F., Cavender-Bares, J., Deacon, N., 2011. Native communities determine the identity of exotic invaders even at scales at which communities are unsaturated. Divers. Distrib. 17, 35–42.
Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Grime, J.P., Mascaro, J., Briggs, J.C., 2011. Don't judge species on their origins. Nature 474, 153.
Derocles, S.A.P., Bohan, D.A., Dumbrell, A.J., Kitson, J.J.N., Massol, F., Pauvert, C., Plantegenest, M., Vacher, C., Evans, D.M., 2018. Biomonitoring for the 21st Century: Integrating Next-Generation Sequencing Into Ecological Network Analysis. Advances in Ecological Research. Academic Press, pp. 1–62.
Deutschewitz, K., Lausch, A., Kühn, I., Klotz, S., 2003. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Glob. Ecol. Biogeogr. 12, 299–311.
Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.
Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, J.R., Medoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C., Caffrey, J.M., 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J. Appl. Ecol. 54, 1259–1267.
Dickey, J.W.E., Cuthbert, R.N., South, J., Britton, J.R., Caffrey, J., Chang, X., Crane, K., Coughlan, N.E., Fadaei, E., Farnsworth, K.D., Ismar-Rebitz, S.M.H., Joyce, P.W.S., Julius, M., Laverty, C., Lucy, F.E., MacIsaac, H.J., McCard, M., McGlade, C.L.O., Reid, N., Ricciardi, A., Wasserman, R.J., Weyl, O.L.F., Dick, J.T.A., 2020. On the RIP: using relative impact potential to assess the ecological impacts of invasive alien species. NeoBiota 55.
Dickie, I.A., Bolstridge, N., Cooper, J.A., Peltzer, D.A., 2010. Co-invasion by Pinus and its mycorrhizal fungi. New Phytol. 187, 475–484.
Dickie, I.A., Cooper, J.A., Bufford, J.L., Hulme, P.E., Bates, S.T., 2017. Loss of functional diversity and network modularity in introduced plant–fungal symbioses. AoB Plants 9.
Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M., Gemmell, N.J., 2005. Are invasive species the drivers of ecological change? Trends Ecol. Evol. 20, 470–474.
Dietz, H., Edwards, P.J., 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology 87, 1359–1367.
Diez, J.M., Sullivan, J.J., Hulme, P.E., Edwards, G., Duncan, R.P., 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecol. Lett. 11, 674–681.
Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N.J., Lososová, Z., Pyšek, P., Richardson, D.M., Molofsky, J., 2018. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat. Commun. 9, 4631.
Domínguez, M.T., Aponte, C., Pérez-Ramos, I.M., García, L.V., Villar, R., Marañón, T., 2012. Relationships between leaf morphological traits, nutrient concentrations and isotopic signatures for Mediterranean woody plant species and communities. Plant Soil 357, 407–424.
Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20.
Drenovsky, R.E., Grewell, B.J., D'Antonio, C.M., Funk, J.L., James, J.J., Molinari, N., Parker, I.M., Richards, C.L., 2012. A functional trait perspective on plant invasion. Ann. Bot. 110, 141–153.
Dubart, M., Alonso, P., Barroso-Bergada, D., Becker, N., Bethune, K., Bohan, D.A., Boury, C., Cambon, M., Canard, E., Chancerel, E., Chiquet, J., David, P., de Manincor, N., Donnet, S., Duputié, A., Facon, B., Guichoux, E., Le Minh, T., Ortiz-Martínez, S., Piouceau, L., Sacco-Martret de Préville, A., Plantegenest, M., Poux, C., Ravigné, V., Robin, S., Trillat, M., Vacher, C., Vernière, C., Massol, F., 2021. Coupling ecological network analysis with high-throughput sequencing-based surveys: Lessons from the next-generation biomonitoring project. Pages 367–430 Advances in Ecological Research - Volume 65. Press, Academic.
Dyderski, M.K., Jagodziński, A.M., 2019. Context-dependence of urban Forest vegetation invasion level and alien species' ecological success. Forests 10, 26.
Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. Annu. Rev. Ecol. Evol. Syst. 41, 59–80.
Elton, C.S., 1958. The Ecology of Invasions by Animals and Plants. Methuen & co ltd., London.
Emery, S.M., Gross, K.L., 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology 88, 954–964.
Escobedo, V.M., Rios, R.S., Salgado-Luarte, C., Stotz, G.C., Gianoli, E., 2017. Disturbance by an endemic rodent in an arid shrubland is a habitat filter: effects on plant invasion and taxonomical, functional and phylogenetic community structure. Ann. Bot. 119, 659–670.
Escoriza, D., Ruhí, A., 2016. Functional distance to recipient communities may favour invasiveness: insights from two invasive frogs. Divers. Distrib. 22, 519–533.
Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A., Pyšek, P., 2011. Socioeconomic legacy yields an invasion debt. Proc. Natl. Acad. Sci. 108, 203–207.
Fargione, J.E., Tilman, D., 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecol. Lett. 8, 604–611.
Fargione, J., Brown, C.S., Tilman, D., 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proc. Natl. Acad. Sci. 100, 8916–8920.
Feng, Y., Fouqueray, T.D., van Kleunen, M., 2019. Linking Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities. J. Ecol. 107, 794–805.
Finerty, G.E., de Bello, F., Bílá, K., Berg, M.P., Dias, A.T.C., Pezzatti, G.B., Moretti, M., 2016. Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. J. Ecol. 104, 1400–1409.
Flinn, K.M., Kuhns, H.A.D., Mikes, J.L., Lonsdorf, E.V., Lake, J.K., 2017. Invasion and succession change the functional traits of serpentine plant communities. J. Torrey Bot. Soc. 144 (109–124), 116.
Flombaum, P., Aragón, R., Chaneton, E.J., 2017. A role for the sampling effect in invaded ecosystems. Oikos 126, 1229–1232.
Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Proches, S., M. van der Bank, Reeves, G., Hedderson, T.A.J., Savolainen, V., 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445, 757–760.
Fournier, A., Penone, C., Pennino, M.G., Courchamp, F., 2019. Predicting future invaders and future invasions. Proc. Natl. Acad. Sci. U. S. A. 116, 7905–7910.
Fridley, J., Stachowicz, J., Naeem, S., Sax, D., Seabloom, E., Smith, M., Stohlgren, T., Tilman, D., Holle, B.V., 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88, 3–17.
Fried, G., Carboni, M., Mahaut, L., Violle, C., 2019. Functional traits modulate plant community responses to alien plant invasion. Perspect. Plant Ecol. Evol. System. 37, 53–63.
Froese, R., Pauly, D., 2021. FishBase. World Wide Web Electronic Publication. http://www.fishbase.org, Version (08/2021).
Fu, H., Zhong, J., Yuan, G., Xie, P., Guo, L., Zhang, X., Xu, J., Li, Z., Li, W., Zhang, M., Cao, T., Ni, L., 2014. Trait-based community assembly of aquatic macrophytes along a water depth gradient in a freshwater lake. Freshw. Biol. 59, 2462–2471.
Funk, J.L., Standish, R.J., Stock, W.D., Valladares, F., 2016. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. Ecology 97, 75–83.
Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. R. Soc. B Biol. Sci. 282, 20142620.
Galland, T., Pérez Carmona, C., Götzenberger, L., Valencia, E., de Bello, F., 2020. Are redundancy indices redundant? An evaluation based on parameterized simulations. Ecol. Indic. 116, 106488.
Gallien, L., Carboni, M., 2017. The community ecology of invasive species: where are we and what's next? Ecography 40, 335–352.
Garibaldi, L.A., Bartomeus, I., Bommarco, R., Klein, A.M., Cunningham, S.A., Aizen, M.A., Boreux, V., Garratt, M.P.D., Carvalheiro, L.G., Kremen, C., Morales, C.L., Schüepp, C., Chacoff, N.P., Freitas, B.M., Gagic, V., Holzschuh, A., Klatt, B.K., Krewenka, K.M., Krishnan, S., Mayfield, M.M., Motzke, I., Otieno, M., Petersen, J., Potts, S.G., Ricketts, T.H., Rundlöf, M., Sciligo, A., Sinu, P.A., Steffan-Dewenter, I., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2015. Trait matching of flower visitors and crops predicts fruit set better than trait diversity. J. Appl. Ecol. 52, 1436–1444.
Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.
Genovesi, P., Carnevali, L., Scalera, R., 2017. The Impact of Invasive Alien Species on Native Threatened Species in Europe. ISPRA M ISSG, Rome.
Gerisch, M., Agostinelli, V., Henle, K., Dziock, F., 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos 121, 508–515.
Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E., Vereecken, N.J., 2017. Massively introduced managed species and their consequences for plant–pollinator interactions. Pages 147-199. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), Advances in Ecological Research vol. 57 - Networks of Invasion: Empirical Evidence and Case Studies. Academic Press.
Gooden, B., French, K., 2015. Impacts of alien plant invasion on native plant communities are mediated by functional identity of resident species, not resource availability. Oikos 124, 298–306.
Gravel, D., Poisot, T., Albouy, C., Velez, L., Mouillot, D., 2013. Inferring food web structure from predator–prey body size relationships. Methods Ecol. Evol. 4, 1083–1090.
Gurevitch, J., Padilla, D.K., 2004. Are invasive species a major cause of extinctions? Trends Ecol. Evol. 19, 470–474.
Hattab, T., Garzón-López, C.X., Ewald, M., Skowronek, S., Aerts, R., Horen, H., Brasseur, B., Gallet-Moron, E., Spicher, F., Decocq, G., Feilhauer, H., Honnay, O., Kempeneers, P., Schmidtlein, S., Somers, B., Van De Kerchove, R., Rocchini, D., Lenoir, J., 2017. A unified framework to model the potential and realized distributions of invasive species within the invaded range. Divers. Distrib. 23, 806–819.
Haubrock, P.J., Pilotto, F., Innocenti, G., Cianfanelli, S., Haase, P., 2021. Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. Glob. Chang. Biol. 27, 606–623.
Hayward, J., Horton, T.R., Pauchard, A., Nuñez, M.A., 2015. A single ectomycorrhizal fungal species can enable a Pinus invasion. Ecology 96, 1438–1444.
Hejda, M., de Bello, F., 2013. Impact of plant invasions on functional diversity in the vegetation of Central Europe. J. Veg. Sci. 24, 890–897.
Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J. Ecol. 97, 393–403.
Helsen, K., Smith, S.W., Brunet, J., Cousins, S.A.O., De Frenne, P., Kimberley, A., Kolb, A., Lenoir, J., Ma, S., Michaelis, J., Plue, J., Verheyen, K., Speed, J.D.M., Graae, B.J., 2018. Impact of an invasive alien plant on litter decomposition along a latitudinal gradient. Ecosphere 9, e02097.
Hooper, D.U., Dukes, J.S., 2010. Functional composition controls invasion success in a California serpentine grassland. J. Ecol. 98, 764–777.

Hulme, P.E., 2007. Biological invasions in Europe: Drivers, pressures, states, impacts and responses. In: Hester, R., Harrison, R.M. (Eds.), Biodiversity Under Threat. Cambridge University Press, Cambridge, UK, pp. 56–80.

Hulme, P.E., Bernard-Verdier, M., 2018a. Comparing traits of native and alien plants: can we do better? Funct. Ecol. 32, 117–125.

Hulme, P.E., Bernard-Verdier, M., 2018b. Evaluating differences in the shape of native and alien plant trait distributions will bring new insights into invasions of plant communities. J. Veg. Sci. 29, 348–355.

Jarzyna, M.A., Jetz, W., 2016. Detecting the Multiple Facets of Biodiversity. Trends Ecol. Evol. 31 (7), 527–538. https://doi.org/10.1016/j.tree.2016.04.002. Epub 2016 May 8.

Jarzyna, M.A., Jetz, W., 2018. Taxonomic and functional diversity change is scale dependent. Nat. Commun. 9, 2565.

Jauni, M., Ramula, S., 2015. Meta-analysis on the effects of exotic plants on the fitness of native plants. Perspect. Plant Ecol. Evol. System. 17, 412–420.

Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., Guralnick, R., Kattge, J., Latimer, A.M., Moorcroft, P., Schaepman, M.E., Schildhauer, M.P., Schneider, F.D., Schrodt, F., Stahl, U., Ustin, S.L., 2016. Monitoring plant functional diversity from space. Natur. Plants 2, 16024.

Johnstone, I.M., 1986. Plant invasion windows: a time-based classification of invasion potential. Biol. Rev. 61, 369–394.

Jordan, N.R., Larson, D.L., Huerd, S.C., 2008. Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. Biol. Invasions 10, 177–190.

Jucker, T., Carboni, M., Acosta, A.T.R., 2013. Going beyond taxonomic diversity: deconstructing biodiversity patterns reveals the true cost of iceplant invasion. Divers. Distrib. 19, 1566–1577.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. 9, 1237–1244.

Kapilkumar, I., Nikolett, G.-S., Hardeep, K., Róbert, G., 2019. Forest type interacts with milkweed invasion to affect spider communities. Insect Conserv. Divers. 12, 321–328.

Kareiva, P., 1996. Developing a predictive ecology for non-indigenous species and ecological invasions. Ecology 77, 1651–1652.

Kashtan, N., Itzkovitz, S., Milo, R., Alon, U., 2004. Topological generalizations of network motifs. Phys. Rev. E 70, 031909.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Carlucci, M. Bergmann, Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C., Dahlin, K.M., Dainese, M., Dalke, I., Fratte, M. Dalle, Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Pereira, C. Maciel Rabelo, Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár V, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Network, T.N., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Garvizu, G. Selaya, Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski Jr., E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Valderrama, M.Y. Vasquez, Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, J., Zheng, J., Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Chang. Biol. 26, 119–188.

Kimball, S., Funk, J.L., Spasojevic, M.J., Suding, K.N., Parker, S., Goulden, M.L., 2016. Can functional traits predict plant community response to global change? Ecosphere 7, e01602.

Klonner, G., Fischer, S., Essl, F., Dullinger, S., 2016. A source area approach demonstrates moderate predictive ability but pronounced variability of invasive species traits. PLoS One 11, e0155547.

Kondratyeva, A., Grandcolas, P., Pavoine, S., 2019. Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. Biol. Rev. 94, 1317–1337.

Kuczynski, L., Grenouillet, G., 2018. Community disassembly under global change: evidence in favor of the stress-dominance hypothesis. Glob. Chang. Biol. 24, 4417–4427.

Kuebbing, S.E., Maynard, D.S., Bradford, M.A., 2018. Linking functional diversity and ecosystem processes: A framework for using functional diversity metrics to predict the ecosystem impact of functionally unique species. J. Ecol. 106, 687–698.

Kulmatiski, A., Beard, K.H., Stevens, J.R., Cobbold, S.M., 2008. Plant–soil feedbacks: a meta-analytical review. Ecol. Lett. 11, 980–992.

Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87, 3186–3199.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol. Lett. 13, 76–86.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: Measuring Functional Diversity From Multiple Traits, and Other Tools for Functional Ecology. R Package Version 1.0-12.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76, 5–13.
Larson, D.L., Bright, J.B., Drobney, P., Larson, J.L., Palaia, N., Rabie, P.A., Vacek, S., Wells, D., 2013. Using prairie restoration to curtail invasion of Canada thistle: the importance of limiting similarity and seed mix richness. Biol. Invasions 15, 2049–2063.
Laureto, L.M.O., Cianciaruso, M.V., Samia, D.S.M., 2015. Functional diversity: an overview of its history and applicability. Natureza & Conservação 13, 112–116.
Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S., Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. J. Veg. Sci. 24, 942–948.
Lee, M.R., Bernhardt, E.S., van Bodegom, P.M., Cornelissen, J.H.C., Kattge, J., Laughlin, D.C., Niinemets, Ü., Peñuelas, J., Reich, P.B., Yguel, B., Wright, J.P., 2017. Invasive species' leaf traits and dissimilarity from natives shape their impact on nitrogen cycling: a meta-analysis. New Phytol. 213, 128–139.
Leffler, A.J., James, J.J., Monaco, T.A., Sheley, R.L., 2014. A new perspective on trait differences between native and invasive exotic plants. Ecology 95, 298–305.
Legendre, P., Gauthier, O., 2014. Statistical methods for temporal and space–time analysis of community composition data. Proc. R. Soc. B Biol. Sci. 281.
Legras, G., Loiseau, N., Gaertner, J.-C., Poggiale, J.-C., Ienco, D., Mazouni, N., Mérigot, B., 2019. Assessment of congruence between co-occurrence and functional networks: a new framework for revealing community assembly rules. Sci. Rep. 9, 19996.
Leishman, M.R., Cooke, J., Richardson, D.M., 2014. Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. J. Ecol. 102, 1451–1461.
Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proc. R. Soc. B Biol. Sci. 283, 20160084.
Lekberg, Y., Gibbons, S.M., Rosendahl, S., Ramsey, P.W., 2013. Severe plant invasions can increase mycorrhizal fungal abundance and diversity. ISME J. 7, 1424–1433.
Leung, B., Drake, J.M., Lodge, D.M., 2004. Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85, 1651–1660.
Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecol. Lett. 7, 975–989.
Lockwood, J.L., Simberloff, D., McKinney, M.L., Von Holle, B., 2001. How many, and which, plants will invade natural areas? Biol. Invasions 3, 1–8.
Loiola, P.P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C.P., Pyšek, P., Lososová, Z., 2018. Invaders among locals: alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. J. Ecol. 106, 2230–2241.
Longo, G., Seidler, T.G., Garibaldi, L.A., Tognetti, P.M., Chaneton, E.J., 2013. Functional group dominance and identity effects influence the magnitude of grassland invasion. J. Ecol. 101, 1114–1124.
Luan, J., Liu, S., Li, S., Whalen, J.K., Wang, Y., Wang, J., Liu, Y., Dong, W., Chang, S.X., 2021. Functional diversity of decomposers modulates litter decomposition affected by plant invasion along a climate gradient. J. Ecol. 109, 1236–1249.
MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86, 42–55.
MacDougall, A.S., Gilbert, B., Levine, J.M., 2009. Plant invasions and the niche. J. Ecol. 97, 609–615.
Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., Villéger, S., 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity. Ecography 2022, e05904. https://doi.org/10.1111/ecog.05904.
Májeková, M., Paal, T., Plowman, N.S., Bryndová, M., Kasari, L., Norberg, A., Weiss, M., Bishop, T.R., Luke, S.H., Sam, K., Le Bagousse-Pinguet, Y., Lepš, J., Götzenberger, L., de Bello, F., 2016. Evaluating functional diversity: missing trait data and the importance of species abundance structure and data transformation. PLoS One 11, e0149270.
Makiola, A., Compson, Z.G., Baird, D.J., Barnes, M.A., Boerlijst, S.P., Bouchez, A., Brennan, G., Bush, A., Canard, E., Cordier, T., Creer, S., Curry, R.A., David, P., Dumbrell, A.J., Gravel, D., Hajibabaei, M., Hayden, B., van der Hoorn, B., Jarne, P., Jones, J.I., Karimi, B., Keck, F., Kelly, M., Knot, I.E., Krol, L., Massol, F., Monk, W.A., Murphy, J., Pawlowski, J., Poisot, T., Porter, T.M., Randall, K.C., Ransome, E., Ravigné, V., Raybould, A., Robin, S., Schrama, M., Schatz, B., Tamaddoni-Nezhad, A., Trimbos, K.B., Vacher, C., Vasselon, V., Wood, S., Woodward, G., Bohan, D.A., 2020. Key questions for next-generation biomonitoring. Front. Environ. Sci. 7.
Maldonado, C., Molina, C.I., Zizka, A., Persson, C., Taylor, C.M., Albán, J., Chilquillo, E., Rønsted, N., Antonelli, A., 2015. Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? Glob. Ecol. Biogeogr. 24, 973–984.
Mammola, S., Carmona, C.P., Guillerme, T., Cardoso, P., 2021. Concepts and applications in functional diversity. Funct. Ecol. 35, 1869–1885.
Mandle, L., Ticktin, T., 2015. Moderate land use changes plant functional composition without loss of functional diversity in India's Western Ghats. Ecol. Appl. 25, 1711–1724.
Martins, G.M., Arenas, F., Neto, A.I., Jenkins, S.R., 2012. Effects of fishing and regional species Pool on the functional diversity of fish communities. PLoS One 7, e44297.
Mason, N.W.H., de Bello, F., 2013. Functional diversity: a tool for answering challenging ecological questions. J. Veg. Sci. 24, 777–780.
Mason, N.W., Mouillot, D., 2013. Functional diversity measures. Encyclopedia of Biodiversity. 3, pp. 597–608.
Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118.
Mason, N.W.H., Lanoiselée, C., Mouillot, D., Irz, P., Argillier, C., 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. Oecologia 153, 441–452.
Mason, T.J., French, K., Jolley, D.F., 2017. Functional richness and identity do not strongly affect invasibility of constructed dune communities. PLoS One 12, e0169243.
Matsuzaki, S.-I.S., Kadoya, T., 2015. Trends and stability of inland fishery resources in Japanese lakes: introduction of exotic piscivores as a driver. Ecol. Appl. 25, 1420–1432.
Matsuzaki, S.-I.S., Sasaki, T., Akasaka, M., 2013. Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. Glob. Ecol. Biogeogr. 22, 1071–1082.
Matsuzaki, S.-I.S., Sasaki, T., Akasaka, M., 2016. Invasion of exotic piscivores causes losses of functional diversity and functionally unique species in Japanese lakes. Freshw. Biol. 61, 1128–1142.
Mazía, N., Chaneton, E.J., Ghersa, C.M., 2019. Disturbance types, herbaceous composition, and rainfall season determine exotic tree invasion in novel grassland. Biol. Invasions 21, 1351–1363.
McCarthy, M.A., Moore, J.L., Morris, W.K., Parris, K.M., Garrard, G.E., Vesk, P.A., Rumpff, L., Giljohann, K.M., Camac, J.S., Bau, S.S., Friend, T., Harrison, B., Yue, B., 2013. The influence of abundance on detectability. Oikos 122, 717–726.
McDonald, T., Gann, G., Jonson, J., Dixon, K., 2016. International standards for the practice of ecological restoration–including principles and key concepts. Society for Ecological Restoration: Washington, DC, USA. Soil-Tec, Inc.,© Marcel Huijser, Bethanie Walder.
McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.
McGrannachan, C.M., McGeoch, M.A., 2019. Multispecies plant invasion increases function but reduces variability across an understorey metacommunity. Biol. Invasions 21, 1115–1129.
McNeish, R.E., Benbow, M.E., McEwan, R.W., 2017. Removal of the invasive shrub, Lonicera maackii (Amur honeysuckle), from a headwater stream riparian zone shifts taxonomic and functional composition of the aquatic biota. Invasive Plant Sci. Manag. 10, 232–246.
MEA, 2005. The Millennium Ecosystem Assessment (www.MAweb.org).
Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K., Yokomizo, H., 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol. Lett. 10, 77–94.
Mérigot, B., Durbec, J.-P., Gaertner, J.-C., 2010. On goodness-of-fit measure for dendrogram-based analyses. Ecology 91, 1850–1859.
Milbau, A.N.N., Nijs, I., 2004. The role of species traits (invasiveness) and ecosystem characteristics (Invasibility) in grassland invasions: a framework. Weed Technol. 18, 1301–1304.
Mirzaie, F.S., Ghorbani, R., Montajama, S., 2013. A comparative study of different biological indices sensitivity: a case study of macroinvertebates of Gomishan Wetland, Iran. World J. Fish Mar. Sci. 5, 611–615.
Mollot, G., Pantel, J.H., Romanuk, T.N., 2017. The effects of invasive species on the decline in species richness: a global meta-analysis. Pages 61-83. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), Advances in Ecological Research vol. 56 - Networks of Invasion: A Synthesis of Concepts. Academic Press.
Mouchet, M., Guilhaumon, F., Villéger, S., Mason, N.W.H., Tomasini, J.A., Mouillot, D., 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. Oikos 117, 794–800.
Mouchet, M.A., Villeger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876.
Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B., Chi, T.D., 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. Oecologia 145 (3), 345–353.
Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177.
Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G.J., Lavorel, S., Le Gall, L., Meslin, L., Morand, S., Morin, X., Morlon, H., Pinay, G., Pradel, R., Schurr, F.M., Thuiller, W., Loreau, M., 2015. Predictive ecology in a changing world. J. Appl. Ecol. 52, 1293–1310.
Murphy, K., Murphy, T.B., 2020. Gaussian parsimonious clustering models with covariates and a noise component. ADAC 14, 293–325.
Murphy, G.E.P., Romanuk, T.N., 2014. A meta-analysis of declines in local species richness from human disturbances. Ecol. Evol. 4, 91–103.
Murphy, H., Westcott, D., Metcalfe, D., 2006. Functional diversity of native and invasive plant species in tropical rainforests. Pages 199–202. 15th Australian Weeds Conference, Papers and Proceedings, Adelaide, South Australia, 24–28 September 2006: Managing Weeds in a Changing Climate. Weed Management Society of South Australia.
Novotny, V., 2009. Beta diversity of plant-insect food webs in tropical forests: a conceptual framework. Insect Conserv. Divers. 2, 5.
Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L., Thuiller, W., 2019. Diversity indices for ecological networks: a unifying framework using hill numbers. Ecol. Lett. 22, 737–747.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package. Pages R Package Version 2.5-7.
O'Leary, B., Burd, M., Venn, S.E., Gleadow, R., 2018. Integrating the Passenger-Driver hypothesis and plant community functional traits to the restoration of lands degraded by invasive trees. For. Ecol. Manag. 408, 112–120.
Ordonez, A., 2014. Global meta-analysis of trait consistency of non-native plants between their native and introduced areas. Glob. Ecol. Biogeogr. 23, 264–273.
Ordonez, A., Wright, I.J., Olff, H., 2010. Functional differences between native and alien species: a global-scale comparison. Funct. Ecol. 24, 1353–1361.
Ouadah, S., Latouche, P., Robin, S., 2022. Motif-based tests for bipartite networks. Electron. J. Stat. 16, 293–330.
Pakeman, R.J., 2014. Functional trait metrics are sensitive to the completeness of the species' trait data? Methods Ecol. Evol. 5, 9–15.

Pakeman, R.J., Quested, H.M., 2007. Sampling plant functional traits: what proportion of the species need to be measured? Appl. Veg. Sci. 10, 91–96.
Pantel, J.H., Bohan, D.A., Calcagno, V., David, P., Duyck, P.F., Kamenova, S., Loeuille, N., Mollot, G., Romanuk, T.N., Thébault, E., Tixier, P., Massol, F., 2017. 14 questions for invasion in ecological networks. Pages 293-340. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), Advances in Ecological Research vol. 56 - Networks of Invasion: A Synthesis of Concepts. Academic Press.
Park, D.S., Potter, D., 2015. Why close relatives make bad neighbours: phylogenetic conservatism in niche preferences and dispersal disproves Darwin's naturalization hypothesis in the thistle tribe. Mol. Ecol. 24, 3181–3193.
Pauchard, A., Milbau, A., Albihn, A., Alexander, J., Burgess, T., Daehler, C., Englund, G., Essl, F., Evengård, B., Greenwood, G.B., Haider, S., Lenoir, J., McDougall, K., Muths, E., Nuñez, M.A., Olofsson, J., Pellissier, L., Rabitsch, W., Rew, L.J., Robertson, M., Sanders, N., Kueffer, C., 2016. Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. Biol. Invasions 18, 345–353.
Pauvert, C., Buée, M., Laval, V., Edel-Hermann, V., Fauchery, L., Gautier, A., Lesur, I., Vallance, J., Vacher, C., 2019. Bioinformatics matters: the accuracy of plant and soil fungal community data is highly dependent on the metabarcoding pipeline. Fungal Ecol. 41, 23–33.
Pavoine, S., 2020. Div: an r package to analyse biodiversity in ecology. Methods Ecol. Evol. 11, 1106–1112.
Pavoine, S., Bonsall, M.B., 2011. Measuring biodiversity to explain community assembly: a unified approach. Biol. Rev. 86, 792–812.
Pavoine, S., Ricotta, C., 2019. Measuring functional dissimilarity among plots: adapting old methods to new questions. Ecol. Indic. 97, 67–72.
Pavoine, S., Ollier, S., Dufour, A.-B., 2005. Is the originality of a species measurable? Ecol. Lett. 8, 579–586.
Pavoine, S., Bonsall, M.B., Dupaix, A., Jacob, U., Ricotta, C., 2017. From phylogenetic to functional originality: guide through indices and new developments. Ecol. Indic. 82, 196–205.
Pearson, D.E., Ortega, Y.K., Eren, Ö., Hierro, J.L., 2018. Community assembly theory as a framework for biological invasions. Trends Ecol. Evol. 33, 313–325.
Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M.A., Melián, C.J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N.E., Gravel, D., 2018. Comparing species interaction networks along environmental gradients. Biol. Rev. 93, 785–800.
Pellock, S., Thompson, A., He, K.S., Mecklin, C.J., Yang, J., 2013. Validity of Darwin's naturalization hypothesis relates to the stages of invasion. Commun. Ecol. 14, 172–179.
Pereira, L.S., Mise, F.T., Tencatt, L.F.C., Baumgartner, M.T., Agostinho, A.A., 2017. Is Coexistence between Non-native and Native Erythrinidae Species Mediated by Niche Differentiation or Environmental Filtering? A case study in the upper Paraná River floodplain, Neotropical Ichthyology, p. 15
Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411.
Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.
Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaëns, T., Deharveng, L., Dubs, F., Joimel, S., Briard, C., Grumiaux, F., Laporte, M.-A., Pasquet, A., Pelosi, C., Pernin, C., Ponge, J.-F., Salmon, S., Santorufo, L., Hedde, M., 2014. Current use of and future needs for soil invertebrate functional traits in community ecology. Basic Appl. Ecol. 15, 194–206.
Pillar, V.D., Blanco, C.C., Müller, S.C., Sosinski, E.E., Joner, F., Duarte, L.D.S., 2013. Functional redundancy and stability in plant communities. J. Veg. Sci. 24, 963–974.
Pocock, M.J.O., Evans, D.M., Memmott, J., 2012. The robustness and restoration of a network of ecological networks. Science 335, 973–977.
Podani, J., Schmera, D., 2006. On dendrogram-based measures of functional diversity. Oikos 115, 179–185.
Poisot, T., Canard, E., Mouillot, D., Mouquet, N., Gravel, D., 2012. The dissimilarity of species interaction networks. Ecol. Lett. 15, 1353–1361.
Powell, K.I., Chase, J.M., Knight, T.M., 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. Am. J. Bot. 98, 539–548.
Powell, K.I., Chase, J.M., Knight, T.M., 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. Science 339, 316–318.
Poyet, M., Eslin, P., Héraude, M., Le Roux, V., Prévost, G., Gibert, P., Chabrerie, O., 2014. Invasive host for invasive pest: when the Asiatic cherry fly (Drosophila suzukii) meets the American black cherry (Prunus serotina) in Europe. Agric. For. Entomol. 16, 251–259.
Poyet, M., Le Roux, V., Gibert, P., Meirland, A., Prévost, G., Eslin, P., Chabrerie, O., 2015. The wide potential trophic niche of the asiatic fruit fly Drosophila suzukii: the key of its invasion success in temperate Europe? PLoS One 10, e0142785.
Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), Biological Invasions. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 97–125
Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95, 1511–1534.
Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Popul. Biol. 21, 24–43.
Rejmánek, M., 1996. A theory of seed plant invasiveness: the first sketch. Biol. Conserv. 78, 171–181.
Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward understanding the ecological impacts of nonnative species. Ecol. Monogr. 83, 263–282.
Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog. Phys. Geogr. Earth Environ. 30, 409–431.
Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytol. 196, 383–396.
Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107.
Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L., Pavoine, S., 2016. Measuring the functional redundancy of biological communities: a quantitative guide. Methods Ecol. Evol. 7, 1386–1395.
Rodriguez, L.F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol. Invasions 8, 927–939.
Romanuk, T.N., Zhou, Y., Brose, U., Berlow, E.L., Williams, R.J., Martinez, N.D., 2009. Predicting invasion success in complex ecological networks. Philos. Trans. R. Soc. B-Biol. Sci. 364, 1743–1754.
Romanuk, T.N., Zhou, Y., Valdovinos, F.S., Martinez, N.D., 2017. Robustness trade-offs in model food webs: Invasion probability decreases while invasion consequences increase with connectance. In: Bohan, D.A., Dumbrell, A.J., Massol, F. (Eds.), Advances in Ecological Research vol. 56 - Networks of Invasion: A Synthesis of Concepts. Academic Press, pp. 263–291.
Roubik, D.W., Villanueva-Gutiérrez, R., 2009. Invasive Africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis. Biological Journal of the Linnean Society 98, 152–160.
Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceauşu, S., Dornelas, M., Hilbers, J.P., Hortal, J., Huijbregts, M.A.J., Navarro, L.M., Schiffers, K.H., Visconti, P., Rondinini, C., 2017. Assessing the suitability of diversity metrics to detect biodiversity change. Biol. Conserv. 213, 341–350.
Santoro, R., Jucker, T., Carboni, M., Acosta, A.T.R., 2012. Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. J. Veg. Sci. 23, 483–494.
Savage, A.M., Rudgers, J.A., Whitney, K.D., 2009. Elevated dominance of extrafloral nectary-bearing plants is associated with increased abundances of an invasive ant and reduced native ant richness. Divers. Distrib. 15, 751–761.
Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. Trends Ecol. Evol. 18, 561–566.
Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I., Rice, W.R., 2007. Ecological and evolutionary insights from species invasions. Trends Ecol. Evol. 22, 465–471.
Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G., Savolainen, V., 2011. Testing Darwin's naturalization hypothesis in the Azores. Ecol. Lett. 14, 389–396.
Schirmel, J., Buchholz, S., 2013. Invasive moss alters patterns in life-history traits and functional diversity of spiders and carabids. Biol. Invasions 15, 1089–1100.
Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80, 469–484.
Schmera, D., Heino, J., Podani, J., Erős, T., Dolédec, S., 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787, 27–44.
Schriever, T.A., Bogan, M.T., Boersma, K.S., Cañedo-Argüelles, M., Jaeger, K.L., Olden, J.D., Lytle, D.A., 2015. Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities. Freshwat. Sci. 34, 399–409.
Selvi, F., Carrari, E., Coppi, A., 2016. Impact of pine invasion on the taxonomic and phylogenetic diversity of a relict Mediterranean forest ecosystem. For. Ecol. Manag. 367, 1–11.
Shuai, F., Lek, S., Li, X., Zhao, T., 2018. Biological invasions undermine the functional diversity of fish community in a large subtropical river. Biol. Invasions 20, 2981–2996.
Simberloff, D., Vitule, J.R.S., 2014. A call for an end to calls for the end of invasion biology. Oikos 123, 408–413.
Simmons, B.I., Cirtwill, A.R., Baker, N.J., Wauchope, H.S., Dicks, L.V., Stouffer, D.B., Sutherland, W.J., 2019. Motifs in bipartite ecological networks: uncovering indirect interactions. Oikos 128, 154–170.
Smith-Ramesh, L.M., Moore, A.C., Schmitz, O.J., 2017. Global synthesis suggests that food web connectance correlates to invasion resistance. Glob. Chang. Biol. 23, 465–473.
Snyder, R.E., Chesson, P., 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecol. Lett. 6, 301–309.
Staab, K., Yannelli, F.A., Lang, M., Kollmann, J., 2015. Bioengineering effectiveness of seed mixtures for road verges: functional composition as a predictor of grassland diversity and invasion resistance. Ecol. Eng. 84, 104–112.
Stachowicz, J.J., Tilman, D., 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. Pages 41-64. In: Sax, D.F., Stachowicz, J.J., Gaines, S.D. (Eds.), Species Invasions: Insights Into Ecology, Evolution and Biogeography. Sinauer Associates.
Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C., Kartesz, J., 2008. The myth of plant species saturation. Ecol. Lett. 11, 313–322.
Stouffer, D.B., Camacho, J., Jiang, W., Amaral, L.A.N., 2007. Evidence for the existence of a robust pattern of prey selection in food webs. Proc. R. Soc. B Biol. Sci. 274, 1931–1940.
Stouffer, D.B., Sales-Pardo, M., Sirer, M.I., Bascompte, J., 2012. Evolutionary conservation of species' roles in food webs. Science 335, 1489–1492.
Stouffer, D.B., Cirtwill, A.R., Bascompte, J., 2014. How exotic plants integrate into pollination networks. J. Ecol. 102, 1442–1450.
Strauss, S.Y., Webb, C.O., Salamin, N., 2006. Exotic taxa less related to native species are more invasive. Proc. Natl. Acad. Sci. 103, 5841–5845.
Strong, J.S., Leroux, S.J., 2014. Impact of non-native terrestrial mammals on the structure of the terrestrial mammal food web of Newfoundland, Canada. PLoS One 9, e106264.
Swanson, H.K., Lysy, M., Power, M., Stasko, A.D., Johnson, J.D., Reist, J.D., 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. Ecology 96, 318–324.
Tan, J., Pu, Z., Ryberg, W.A., Jiang, L., 2015. Resident-invader phylogenetic relatedness, not resident phylogenetic diversity, controls community invasibility. Am. Nat. 186, 59–71.

Taudiere, A., Violle, C., 2016. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. Ecography 39, 699–708. https://doi.org/10.1111/ecog.01433.

Tedersoo, L., Suvi, T., Beaver, K., Kõljalg, U., 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native Vateriopsis seychellarum (Dipterocarpaceae) and Intsia bijuga (Caesalpiniaceae) to the introduced Eucalyptus robusta (Myrtaceae), but not Pinus caribea (Pinaceae). New Phytol. 175, 321–333.

Thomas, C.D., Palmer, G., 2015. Non-native plants add to the British flora without negative consequences for native diversity. Proc. Natl. Acad. Sci. 112, 4387–4392.

Thomsen, M.S., Wernberg, T., Olden, J.D., Griffin, J.N., Silliman, B.R., 2011. A framework to study the context-dependent impacts of marine invasions. J. Exp. Mar. Biol. Ecol. 400, 322–327.

Thomsen, M.S., Byers, J.E., Schiel, D.R., Bruno, J.F., Olden, J.D., Wernberg, T., Silliman, B.R., 2014. Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Mar. Ecol. Prog. Ser. 495, 39–47.

Thukral, A.K., 2017. A review on measurement of alpha diversity in biology. Agric. Res. J. 54, 1–10.

Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78, 81–92.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Tölgyesi, C., Török, P., Kun, R., Csathó, A.I., Bátori, Z., Erdős, L., Vadász, C., 2019. Recovery of species richness lags behind functional recovery in restored grasslands. Land Degrad. Dev. 30, 1083–1094.

Tomasetto, F., Duncan, R.P., Hulme, P.E., 2019. Resolving the invasion paradox: pervasive scale and study dependence in the native-alien species richness relationship. Ecol. Lett. 22, 1038–1046.

Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P.A., Brosse, S., Villéger, S., 2018. Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. Ecol. Lett. 21, 1649–1659.

Trøjelsgaard, K., Jordano, P., Carstensen, D.W., Olesen, J.M., 2015. Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. Proc. R. Soc. B Biol. Sci. 282, 20142925.

Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Grenyer, R., Helmus, M.R., Jin, L.S., Mooers, A.O., Pavoine, S., Purschke, O., Redding, D.W., Rosauer, D.F., Winter, M., Mazel, F., 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biol. Rev. 92, 698–715.

Ulmer, R., Couty, A., Eslin, P., Chabrerie, O., 2021. Effect of macroarthropods on Drosophila suzukii peri-oviposition events: an experimental screening. Entomologia Experimentalis et Applicata 169, 519–530.

Vacher, C., Tamaddoni-Nezhad, A., Kamenova, S., Peyrard, N., Moalic, Y., Sabbadin, R., Schwaller, L., Chiquet, J., Smith, M.A., Vallance, J., Fievet, V., Jakuschkin, B., Bohan, D.A., 2016. Learning ecological networks from next-generation sequencing data. In: Woodward, G., Bohan, D.A. (Eds.), Advances in Ecological Research. Academic Press, pp. 1–39.

Valéry, L., Fritz, H., Lefeuvre, J.-C., 2013. Another call for the end of invasion biology. Oikos 122, 1143–1146.

Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M., Fischer, M., 2010a. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecol. Lett. 13, 947–958.

Van Kleunen, M., Weber, E., Fischer, M., 2010b. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13, 235–245.

Van Wilgen, N.J., Richardson, D.M., 2011. Is phylogenetic relatedness to native species important for the establishment of reptiles introduced to California and Florida? Divers. Distrib. 17, 172–181.

Vandepitte, K., de Meyer, T., Helsen, K., van Acker, K., Roldán-Ruiz, I., Mergeay, J., Honnay, O., 2014. Rapid genetic adaptation precedes the spread of an exotic plant species. Mol. Ecol. 23, 2157–2164.

Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Médail, F., Moragues, E., Traveset, A., Troumbis, A.Y., Hulme, P.E., 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J. Biogeogr. 33, 853–861.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Glob. Ecol. Biogeogr. 22, 671–681.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892.

Wang, C., Jiang, K., Liu, J., Zhou, J., Wu, B., 2018. Moderate and heavy Solidago canadensis L. invasion are associated with decreased taxonomic diversity but increased functional diversity of plant communities in East China. Ecol. Eng. 112, 55–64.

Wang, C., Wu, B., Jiang, K., Zhou, J., Du, D., 2019. Canada goldenrod invasion affect taxonomic and functional diversity of plant communities in heterogeneous landscapes in urban ecosystems in East China. Urban For. Urban Green. 38, 145–156.

Wardle, D.A., 2001. Experimental demonstration that plant diversity reduces invasibility – evidence of a biological mechanism or a consequence of sampling effect? Oikos 95, 161–170.

Wei, Z., Yang, T., Friman, V.-P., Xu, Y., Shen, Q., Jousset, A., 2015. Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. Nat. Commun. 6, 8413.

Williamson, M., 1996. Biological invasions (Chapman & Hall London).

Wong, M.K.L., Guénard, B., Lewis, O.T., 2019. The cryptic impacts of invasion: functional homogenization of tropical ant communities by invasive fire ants. BioRxiv:611749.

Zettlemoyer, M.A., Schultheis, E.H., Lau, J.A., 2019. Phenology in a warming world: differences between native and non-native plant species. Ecol. Lett. 22, 1253–1263.

Zhao, T., Villéger, S., Cucherousset, J., 2019. Accounting for intraspecific diversity when examining relationships between non-native species and functional diversity. Oecologia 189, 171–183.